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Understanding Patterns In Nature

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Abstract

Nature is full of interesting patterns. One of the most important tasks across the natural sciences, especially the biological sciences, is to identify and explain real patterns in nature. This dissertation provides a philosophical investigation of the nature and roles of real patterns in biological inquiry and the various strategies that biologists employ to explain and understand real patterns in nature. In Chapter 1, I advocate for a pragmatic approach to the reality of patterns in data. I argue that patterns in data are expected to play different scientific roles in different research contexts and that a pattern in data is real if and only if it fulfills the scientific role it is expected to play in a specific research context. In Chapter 2, I give a critical evaluation of the use and limitations of null-model-based hypothesis testing as a research strategy to explain patterns in the biological sciences. I argue that null-model-based hypothesis testing fails to work as a proper analog to traditional statistical null-hypothesis testing as used in well-controlled experimental research, and that the random process hypothesis should not be privileged as a null hypothesis. Instead, the possible use of the null model resides in its role of providing a way to challenge scientists' commonsense judgments about how a seemingly unusual pattern could have come to be. In Chapter 3, I clarify the definition of a baseline model and apply it to the niche-neutral debate about how to understand biodiversity patterns. I argue that from a process-based perspective, a neutral model in ecology should not be regarded as a baseline model relative to classical niche-based models. In Chapter 4, I investigate the testability and the scientific value of the notion of overall relative causal importance by carefully examining the controversy over empirical adaptationism in evolutionary biology. My analysis of the case of empirical adaptationism provides reasons for scientists to reconsider the value and necessity of engaging in scientific debates involving the notion of overall relative causal importance.

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UNDERSTANDING PATTERNS IN NATURE

Dedication

For my beloved family

(my mother Guo'ai Liu 刘国爱, my father Changli Zhang 张昌利,

my brother Yingjun Zhang 张颖君, and my nephew Yuwei Zhang 张育玮)

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ABSTRACT

UNDERSTANDING PATTERNS IN NATURE

Mingjun Zhang

Michael Weisberg

Nature is full of interesting patterns. One of the most important tasks across the natural sciences, especially the biological sciences, is to identify and explain real patterns in nature. This dissertation provides a philosophical investigation of the nature and roles of real patterns in biological inquiry and the various strategies that biologists employ to explain and understand real patterns in nature. In Chapter 1, I advocate for a pragmatic approach to the reality of patterns in data. I argue that patterns in data are expected to play different scientific roles in different research contexts and that a pattern in data is real if and only if it fulfills the scientific role it is expected to play in a specific research context. In Chapter 2, I give a critical evaluation of the use and limitations of *null-model-based hypothesis testing* as a research strategy to explain patterns in the biological sciences. I argue that null-model-based hypothesis testing fails to work as a proper analog to traditional statistical null-hypothesis testing as used in well-controlled experimental research, and that the random process hypothesis should not be privileged as a null hypothesis. Instead, the possible use of the null model resides in its role of providing a way to challenge scientists' commonsense judgments about how a seemingly unusual pattern could have come to be. In Chapter 3, I clarify the definition of a baseline model and apply it to the niche-neutral debate about how to understand biodiversity patterns. I argue that from a process-based perspective, a neutral model in ecology should not be regarded as a baseline model relative to classical niche-based models. In Chapter 4, I investigate the testability and the scientific value of the notion of *overall relative causal importance* by carefully examining the controversy over empirical adaptationism in evolutionary biology. My analysis of the case of empirical adaptationism provides reasons for scientists to reconsider the value and necessity of engaging in scientific debates involving the notion of overall relative causal importance.

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Introduction

Nature is complex, yet also full of interesting patterns. One of the most important tasks across the natural sciences, especially the biological sciences, is to identify and explain real patterns in nature. As Robert MacArthur (1972, p. 1), one of the most important figures in modern ecology, once said, "To do science is to search for repeated patterns, not simply to accumulate facts […]". Despite this importance, the concept of pattern has received relatively little philosophical attention. In an attempt to bridge this gap, this dissertation provides a philosophical investigation of the nature and roles of real patterns in biological inquiry and the various strategies that biologists employ to explain and understand real patterns in nature.

This dissertation consists of four major chapters. The first chapter addresses the question of what counts as a real pattern. The second and third chapters provide critical examinations of two important research strategies that biologists use to explain patterns in nature: null-model-based hypothesis testing and baseline modeling. The fourth chapter examines the notion of the overall relative causal importance of pattern-generating factors. Each chapter is an article that can be read independently, but all of them are still thematically connected by their focus on the conceptual and methodological issues in the study of biological patterns.

For many researchers, identifying real patterns from data is the starting point of their work. However, theoretically speaking, one can identify infinitely many patterns from one and the same data set. Are all these patterns real? If not, how should we distinguish real patterns from unreal ones? In Chapter 1, I advocate for a pragmatic

approach to the reality of patterns in data. I argue that (a) patterns in data are expected to play different scientific roles in different research contexts and (b) a pattern in data is real if and only if it fulfills the scientific role that it is expected to play in a specific research context. More specifically, I distinguish among three scientific roles that patterns in data can play in scientific inquiry: (1) Patterns can serve as efficient compressed representations of data in data description, storage, and transmission; (2) patterns in data can serve as evidence for the existence of scientific phenomena; (3) patterns in data can serve as targets of systematic explanation. For each of these roles, I elaborate the criteria for evaluating the reality of patterns in data. Then I consider an alternative account of patterns in data – McAllister's stipulationist view – and discuss some of the problems of this view through the lens of the pragmatic approach.

When faced with a pattern that requires an explanation, biologists usually appeal to specific causal processes or mechanisms, but sometimes the pattern under investigation may just be an arrangement that occurs by chance. Given this, some researchers argue that in order to demonstrate that a particular process or mechanism is responsible for the formation of a certain pattern, one needs to first build a null model based on a randomization procedure and then try to reject the null hypothesis that the pattern under investigation is the result of random processes. I call this research strategy *null-model-based hypothesis testing*.

In Chapter 2, I give a critical evaluation of the use and limitations of null-model-based hypothesis testing as a research strategy in the biological sciences. Using as an example the controversy over the use of null hypotheses and null models in species co-occurrence studies, I argue that null-model-based hypothesis testing fails to work as a

proper analog to traditional statistical null-hypothesis testing as used in well-controlled experimental research, and that the random process hypothesis should not be privileged as a null hypothesis. Instead, the possible use of the null model resides in its role of providing a way to challenge scientists' commonsense judgments about how a seemingly unusual pattern could have come to be. Despite this possible use, null-model-based hypothesis testing still carries certain limitations, and it should not be regarded as an obligation for biologists who are interested in explaining patterns in nature to first conduct such a test before pursuing their own hypotheses.

Community ecology is the study of patterns in the diversity, abundance, and composition of species in ecological communities as well as the processes underlying these patterns. One of the patterns that are of interest to community ecologists is the pattern of relative species abundance, which describes the relative commonness or rarity of different species on the same trophic level of an ecological community. The traditional way to explain this pattern is to examine niche differences, i.e., the different ways that different species use resources in a certain environment. Proponents of neutral models have challenged this approach by arguing that species differences may not be essential for explaining patterns of relative species abundance, and that those patterns can be explained by building a neutral model which ignores the niche differences among species and considers instead processes such as random reproduction, death, immigration, and speciation. One way to justify the use of neutral models in ecology is to regard a neutral model as a baseline model based on which more complicated models can be constructed.

In Chapter 3, I give a critical examination of the claim that neutral models of biodiversity can be used as baseline models in community ecology. I define Model A as a

baseline model relative to Model B if and only if A contains necessary factors that must also be considered in B in order to address certain type(s) of phenomena in a domain, and B can be constructed by adding more complexity into A. Based on this characterization, I argue that whether a model counts as a baseline model depends on what type of phenomena it is intended to address and which models it is compared with. In the debate between neutral theory and niche-based theory, a neutral model should not be regarded as a baseline model relative to classical niche-based models from a process-based perspective. As an implication, neutral models do not have methodological priority over niche-based models.

Phenomena in biology are usually influenced by more than one causal factor. In many cases, the question is not about which single factor provides *the* correct explanation for a phenomenon, but about which causal factor plays a *more important* role in the production of the phenomenon. Debates about relative causal importance can happen at the level of individual cases, but more often they involve the overall relative causal importance of different factors at a more general level, such as at the level of the totality of phenomena in a domain. For example, in the long-standing nature-nurture debate, scientists disagree on whether genetic or environmental factors are generally more important in human development. While debates about overall relative causal importance are common in scientific discourse, philosophical issues concerning this notion have received relatively little attention.

In Chapter 4, I give a critical evaluation of the testability and the scientific value of the notion of overall relative causal importance by carefully examining the controversy over empirical adaptationism in evolutionary biology. Roughly speaking, empirical

adaptationism is the view that natural selection is, in most cases, the most (or the only) important cause of evolution compared with other evolutionary factors. Philosophers and biologists who have tried to formulate empirical adaptationism usually share (explicitly or implicitly) two assumptions: (1) Empirical adaptationism, while its truth is currently unknown or controversial, is an empirical claim about nature that is *scientifically testable* in the long run; (2) empirical adaptationism is *worth testing*. In this chapter, I reexamine these two assumptions and argue that both are mistaken given how empirical adaptationism is currently formulated. A series of conceptual and methodological difficulties makes testing empirical adaptationism in a biologically non-arbitrary way virtually impossible. Moreover, those who argue in favor of testing empirical adaptationism have yet to demonstrate the distinctive value as well as the necessity of conducing such a test. My analysis of the case of empirical adaptationism also provides reasons for scientists to reconsider the value and necessity of engaging in scientific debates involving the notion of overall relative causal importance.

Chapter 1: What is a real pattern?
A pragmatic approach to the reality of patterns in data

1. Introduction

It is a common view that any data set can be thought of as containing two components: a relatively simple pattern that shows certain features or order of data, and a certain level of noise or deviation which indicates the discrepancy between the pattern and the data (McAllister, 1997). An important part of scientific inquiry involves identifying real patterns from data. However, theoretically speaking, one can identify infinitely many patterns from one and the same data set. This fact raises a series of philosophical questions concerning the nature of real patterns: Are all patterns exhibited by a data set real? If not, how should we distinguish real patterns from unreal ones? In one data set, is there only a single real pattern or multiple real ones? If there can be multiple real patterns in one data set, are they equally real? Is it even reasonable to compare the realness of patterns?

In this chapter, I attempt to address some of these issues by advocating a pragmatic approach to the reality of patterns in data. I will argue that (1) patterns in data are expected to play different scientific roles in different research contexts and (2) a pattern in data is real if and only if it fulfills the scientific role that it is expected to play in a specific research context. First, I give a general introduction of the pragmatic approach and list three kinds of scientific roles that patterns in data can play in science. Second, I will elaborate each of these roles of real patterns in more detail and show how they feature in scientific inquiry. Then, I will come back to the issues raised by the

multiplicity of patterns in data and introduce McAllister's response to this issue based on a stipulationist view of patterns in data. Finally, I will show how McAllister's stipulationist view is problematic when we take into consideration the different roles of patterns in science and how the problems faced by the stipulationist view might be addressed under the pragmatic approach I suggest.

2. A pragmatic approach to the reality of patterns in data

One major problem with philosophical discussions of the reality of patterns in data is that philosophers fail to distinguish among very different roles that patterns are expected to play in science. Given different roles assigned to patterns, there can be different criteria for what counts as a real pattern. I distinguish among three scientific roles that patterns in data can play in scientific inquiry.[1]

> (1) Patterns serve as efficient compressed representations of data in the description, storage, and transmission of data.
>
> (2) Patterns in data serve as evidence for the existence of scientific phenomena in data-to-phenomena reasoning.
>
> (3) Patterns in data serve as targets of systematic explanation.

In the following three sections, I will elaborate each of these roles of real patterns in more detail. As we shall see, there is no single, over-arching account of real patterns. Different research goals attribute different roles to patterns in data, which involve different criteria with respect to the reality of patterns. This fact precludes a single account of real patterns.

[1] I do not mean to suggest that this list is exhaustive. However, in reviewing the literature, these epistemic roles of real patterns are particularly apparent.

3. Real patterns as efficient compressed representations of data

Suppose that you obtain a long string of numbers with some special importance, and you have to report it to your colleague over the phone in very limited time. What would you do? A sensible strategy would be to try to identify a pattern in those numbers – if possible – and report the pattern, rather than each number, to your colleague. In this context, the pattern works as an efficient description of data in the process of data transmission. In a well-known discussion of real patterns, philosopher Daniel Dennett (1991) expresses a similar idea: He thinks that "a series is not random – has a pattern – if and only if there is some more efficient way of describing it" (p. 32).

Dennett's account of real patterns is inspired by the mathematician and computer scientist Gregory Chaitin's discussion about the nature of randomness. Chaitin (1975) proposes what he calls the "algorithmic definition" of randomness as follows:

> A series of numbers is random if the smallest algorithm capable of specifying it to a computer has about the same number of bits of information as the series itself. (p. 48)

In other words, a series of numbers is random if a more efficient algorithm of specifying the series does not exist. One important conclusion of Chaitin's discussion of randomness is that although randomness can be defined, the randomness of a specific series of digits is *unprovabl*e. This is because in order to show that a series of digits is random, one must prove that a more efficient algorithm of describing the series does not exist. But such a proof, according to Gödel's incompleteness theorem, cannot be obtained. This finding is used by Chaitin to demonstrate the limitations of what can be done in mathematics.

Fortunately, although the randomness of a series of digits is unprovable, it is possible to demonstrate that a particular series of digits is *nonrandom* – has a pattern – if

one can find a more efficient algorithm of describing the series. This fact allows Dennett (1991) to develop an account of real patterns as follows:

> A pattern exists in some data – is real – if *there is* a description of the data that is more efficient than the bit map, whether or not anyone can concoct it. (p. 34)

Here a "bit map" refers to a verbatim description of data, and any data description that is more efficient than the bit map is a description of a real pattern in data. For example, since "01010101010101010101" can be efficiently described as "01 repeated ten times," we can say that, according to Dennett's account, there exists a real pattern in this string of numbers.

Central to this understanding of real patterns is the notion of compressibility. When a more efficient description of data exists, the data is said to be *compressible*, and the pattern works as a compressed representation of that data. Given this, we can say that Dennett provides a *compression-based* account of real patterns. Notice that, according to this account, the transformation between data and real pattern should be two-way symmetrical: If it is possible to identify a real pattern given a data set, then it should also be possible to regenerate the data given the description of that pattern, and vice versa (Millhouse, 2020, p. 5). For example, if we are told that the description "01 repeated ten times, except that the sixth digit is 1" reveals a real pattern in a string of numbers, then we are able to retrieve the original string "01010111010101010101." The transformation process from data to pattern (i.e., its compressed representation) can be called *compression*, and the reverse process *decompression*.

Under the compression-based account, real patterns are expected to serve as *efficient compressed representations* of data. Since the goal of identifying such real

patterns is to find more efficient ways of describing data so as to facilitate data storage or transmission, a pattern is real if and only if it helps to achieve this goal.

What if there is more than one efficient way to describe a data set? If we adopt the compression-based account of real patterns, then all of these efficient descriptions are descriptions of real patterns. When there are multiple real patterns in the same data set, one may wonder whether it is reasonable to compare their realness and claim one pattern to be "more real" than another. The answer depends on how to define the degree of realness of a pattern. If it is defined in terms of the extent to which a data set is compressed, then claiming a pattern to be more real than another is simply a different way to say that the former pattern provides a more efficient way to describe a data set, and there is no deeper meaning to the notion of "more real" here.

There are two salient features of the compression-based account of real patterns. One is that it is *empirically indifferent*: It does not consider the origin of data but depends entirely on a formal criterion, namely, the compressibility of data (Chaitin, 1975, p. 47). Since how the data were produced is not part of the criterion for deciding the reality of a pattern, it does not matter whether the data under consideration were manually made up, generated by a computer, or collected with complex scientific instruments in a well-designed experiment.

Another feature of this account is that it regards the reality of a pattern as data-set-specific. Whether a pattern is real or not depends solely on the features of the focal data set. It does not matter whether the same pattern can also be identified in other data sets.

4. Real patterns in data as evidence for scientific phenomena

As argued in the last section, the compression-based account of real patterns is purely formal and empirically indifferent. While this account of real patterns is important in mathematical and computational sciences, it is less so in many other domains, especially those dealing with data produced through carefully designed experiments or highly structured observation schemes. Instead of serving as efficient compressed representations of data, in these cases, patterns in data are primarily used as evidence for the existence of scientific phenomena. My analysis of this role of patterns in data will build on a critical reading of Bogen and Woodward's three-tiered framework concerning the relationship among data, phenomena, and theories in science.

4.1 Data, phenomena, and theories: Bogen and Woodward's three-tiered framework

In a series of papers (Bogen and Woodward, 1988, 1992; Woodward, 1989, 2000, 2010, 2011), Bogen and Woodward introduced and defended a distinction between data and phenomena in scientific inquiry.

According to Woodward (1989), data are "what registers on a measurement or recording device in a form which is accessible to the human perceptual system, and to public inspection" (p. 394). In his latest restatement and defense of the data/phenomena distinction, Woodward (2011) similarly defines data as "public records produced by measurement and experiment" (p. 166). By contrast, phenomena are "features of the world that in principle could recur under different contexts or conditions" (Woodward, 2011, p. 166); they can be "detected through the use of data, but in most cases are not observable in any interesting sense of that term" (Bogen and Woodward, 1988, p. 306).

Bogen and Woodward use a number of examples to illustrate this distinction between data and phenomena. Consider the case of measuring the melting point of a metal, such as lead. To determine the melting point of lead, one needs to use the same measuring instrument (such as a certain kind of thermometer) to conduct a series of measurements on the same sample. In this case, the thermometer readings constitute data, while the melting point, which is a property of lead, is the phenomenon.

Also, consider the case of detecting weak neutral currents. Weak neutral currents occur in subatomic interactions mediated by particles called Z bosons. While a weak neutral current interaction is not directly observable by the human sensory system, it produces electrically charged particles that can be detected by a bubble chamber. A bubble chamber is a vessel filled with a superheated transparent liquid. When an electrically charged particle passes through a bubble chamber, the superheated liquid vaporizes and forms bubbles, thereby marking the track of the particle. In this case, photographs of bubble chamber tracks are data, while weak neutral currents are the phenomenon.

Based on the distinction between data and phenomena, Bogen and Woodward advocate a three-tiered framework concerning the relationship among data, phenomena, and theories (see Figure 1-1 for an illustration):

> (1) Scientific theories are expected to provide systematic explanations for phenomena; the existence of phenomena is used as evidence for scientific theories.
> (2) Phenomena under investigation, along with other causal factors involved in the process of phenomenon detection, cause data. Data serve as evidence for the existence of phenomena.

Figure 1-1. The data-phenomena-theory framework advocated by Bogen and Woodward

To see how this framework works, consider the two examples mentioned above. In the case of measuring the melting point of lead, the melting point is not determined by making a single measurement, but estimated by using the mean of a series of thermometer readings. These readings, which constitute data, serve as evidence for the phenomenon, but they are not themselves objects of systematic explanation. Each recorded thermometer reading is influenced by many other factors besides the melting point of lead, such as the time that the measurer begins to record the thermometer reading, the relative position of the thermometer and the sample, and the slight fluctuations of temperature and atmospheric pressure in the environment of measurement. A scientific theory, such as a theory of molecular structure, is expected to explain why the melting point of lead in certain environmental conditions is approximately 327.5 degrees Celsius. But it is unnecessary and usually impossible for such a theory to explain why a particular thermometer reading occurs.

Bogen and Woodward's framework also applies in the case of detecting weak neutral currents. In this case, bubble chamber photographs serve as evidence for the existence of weak neutral currents, which in turn provides crucial evidence for the Weinberg-Salam theory. The Weinberg-Salam theory, which unifies the weak and electromagnetic forces, predicts and explains the existence of weak neutral currents, but it

cannot and is not expected to provide systematic explanations for the details of each bubble chamber photograph.

4.2 Counterfactual dependence in data-to-phenomena reasoning

Let us focus on the evidential role of data in data-to-phenomena reasoning. Woodward (2000) argues that in order for data to play their evidential role, a right sort of counterfactual dependence relationship should hold between data and the phenomenon-claim for which the data are to provide evidence. To illustrate the notion of counterfactual dependence, consider a relatively simple case of phenomenon detection. Suppose that P_1 and P_2 are two competing, mutually exclusive claims about a phenomenon; D_1 and D_2 are two possible data outcomes produced in the process of trying to detect the phenomenon of interest. In order for data to play their evidential role of distinguishing between P_1 and P_2, in an ideal case the following counterfactual dependence relationships are expected to obtain:

(a) D_1 is produced when and only when P_1 is true.
(b) D_2 is produced when and only when P_2 is true.

When (a) and (b) hold, we can make inferences as follows:

(c) If D_1 is produced, conclude that P_1 is true.
(d) If D_2 is produced, conclude that P_2 is true.

Notice that (a) is stronger than the requirement that P_1 is sufficient for the production of D_1. This is because if P_2 is also sufficient for the production of D_1, then D_1 is not able to help discriminate between P_1 and P_2 and provide evidence for P_1. The same point holds for (b). It also needs to be recognized that what is described above is an ideal case. In

practice, there can be more than two competing, mutually exclusive claims about a phenomenon of interest, and the satisfaction of the counterfactual dependence relationships can come in degrees.

Several issues need to be clarified in order to make the counterfactual dependence requirement work in practice. First, does D_1 (or D_2) refer to a *particular* data outcome or a *type* of data outcome? The production of data is influenced by many other causal factors besides the phenomenon of interest. Since it is unlikely to keep the states of all the relevant causal factors exactly the same across different rounds of data collection, data collected in different rounds are unlikely to be exactly the same even in well-designed and controlled studies. Hence, D_1 (or D_2) should be understood as a type, rather than a particular instance, of data outcome.

Second, if D_1 (or D_2) should be understood as a type of data outcome, how could scientists tell whether a particular data outcome is an instance of D_1 or D_2? The answer to this question is essential for evidential reasoning from data to phenomena: If the counterfactual dependence relations between data and phenomenon-claims tell us that "if D_1 is produced, conclude that P_1 is true; if D_2 is produced, conclude that P_2 is true," then at least in principle there should be some way to determine whether a particular data outcome is an instance of D_1 or D_2. But how is this done? I will address this issue in the following section.

4.3 Locating the role of patterns in data-to-phenomena reasoning

Since it is unlikely to obtain exactly the same data even in well-controlled experiments, the indicator of the type of a data outcome should go beyond the features of specific data

points. I suggest that this indicator be a characteristic pattern in data. Patterns in this context are understood as representations of data which show certain features or order of data, and it is possible for multiple non-identical data sets to exhibit the same pattern. Given this, we can modify the counterfactual dependence relationships involved in data-to-phenomena reasoning as follows.

Suppose that P_1 and P_2 are two competing, mutually exclusive claims about a phenomenon of interest. PA_1 and PA_2 are patterns in data that are predicted to correspond to P_1 and P_2 respectively. In order for data to play their evidential role of distinguishing between P_1 and P_2 under certain settings, the following counterfactual dependence relationships are expected to obtain:

(a*) PA_1 is exhibited in data when and only when P_1 is true.
(b*) PA_2 is exhibited in data when and only when P_2 is true.

When (a*) and (b*) hold, we can make inferences as follows:

(c*) If PA_1 is exhibited in data, conclude that P_1 is true.
(d*) If PA_2 is exhibited in data, conclude that P_2 is true.

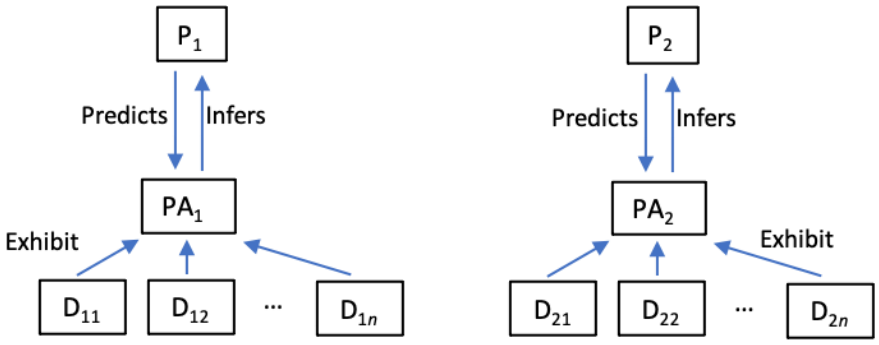


Figure 1-2. The counterfactual dependence relationships between phenomenon-claims and patterns in data

Figure 1-2 is an illustration of these modified counterfactual dependence relationships. As shown in Figure 1-2, it is possible for different data outcomes (e.g., D_{11},

D_{12}, …) to exhibit the same pattern (e.g., PA_1). When some data do exhibit a characteristic pattern that is predicted to correspond to a phenomenon-claim, those data can be used as evidence for that phenomenon-claim. In other words, patterns in data serve as a *steppingstone* for data to play their evidential role in data-to-phenomena reasoning.

Taking patterns into consideration in data-to-phenomena reasoning helps "dissolve" an issue mentioned above. Instead of asking whether a particular data set is an instance of a type of data outcome, what matters is whether this data set exhibits the characteristic pattern that is thought to correspond to the phenomenon of interest. This renders unnecessary the extra step of determining the "type" of a particular data outcome in data-to-phenomena reasoning.

To see how patterns actually feature in data-to-phenomena reasoning, consider the case of measuring the melting point of lead again. Given previous studies on other metals' properties, it is reasonable to assume that lead has a fixed melting point under certain environmental conditions. But under what conditions could the data support this claim? To measure the melting point of lead, researchers make a series of measurements of the temperature of a lead sample when it is melting; this process yields a series of temperature readings. If lead does have a fixed melting point under certain environmental conditions, and assuming that there is no systematic error in the measurement, then the data points (i.e., the thermometer readings) would be expected to be more or less normally distributed. When the temperature readings do exhibit a normal distribution pattern, the required counterfactual dependence relationship between the pattern and the phenomenon-claim is satisfied. In this case, temperature readings can work as evidence for the phenomenon-claim that lead has a fixed melting point under certain environmental

conditions, and the mean of the distribution can be used as an estimation of the true melting point of lead. However, if the temperature readings fail to exhibit a normal distribution pattern, but exhibit, say, a multimodal distribution, then the data cannot serve as evidence for the phenomenon-claim of interest, and the mean of the whole data distribution also becomes physically meaningless.

Similar points also apply in the case of detecting weak neutral currents. In experiments designed to detect such a phenomenon at CERN (European Organization for Nuclear Research) between 1972-1973, researchers obtained about 290,000 bubble chamber photographs as data, but only 100 or so of them were thought to provide evidence for the existence of weak neutral currents. The key to identifying such photographs is to look for characteristic patterns of particle tracks that are predicted to appear if weak neutral currents really exist. Weak neutral currents can be produced in many kinds of interactions. One example is the case where a neutrino strikes a nucleon, which produces another neutrino and a shower of strongly interacting particles. While neutrinos, which are electrically neutral, cannot leave tracks in a bubble chamber, the strongly interacting particles produced in the above case, which are electrically charged, can leave tracks, and these tracks show certain characteristic patterns. Hence, only when bubble chamber photographs exhibit such characteristic patterns of particle tracks, can they be thought to provide evidence for the occurrence of weak neutral currents.

My emphasis of the role of patterns in data-to-phenomenon reasoning is not intended to be a denial of Bogen and Woodward's data-phenomena distinction, but a complement to their framework based on such a distinction. The aim here is to make *explicit* the role of patterns in data-to-phenomena reasoning and incorporate it into Bogen

and Woodward's framework. If my analysis is right, then the three-tiered framework advocated by Bogen and Woodward should be complemented as a four-tiered one involving the relationship among data, *patterns in data*, phenomena, and scientific theories (see Figure 1-3).

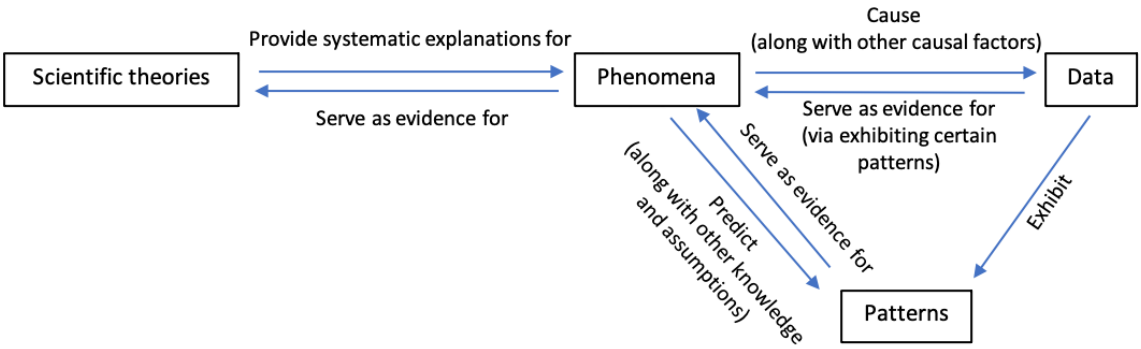


Figure 1-3. A four-level framework involving data, patterns, phenomena, and scientific theories

4.4 Real vs. unreal patterns in the context of phenomenon detection

In phenomenon detection, data play their evidential role via exhibiting certain characteristic patterns that correspond to the phenomena of interest. In this context, a pattern is real if and only if it is exhibited by the data to an extent that satisfies the criterion concerning allowable noise levels and it is indeed caused by the phenomenon of interest.

Data may fail to play their evidential role in two ways. First, data may fail to exhibit the characteristic pattern that is predicted to correspond to the phenomenon of interest, given certain specified standards concerning allowable noise levels. Second, the expected pattern is exhibited by the relevant data to a great enough extent, but it results from factors other than the phenomenon of interest. It is in this case that the notion of

unreal (or bogus) pattern becomes relevant. A pattern is said to be unreal when it mimics the characteristic pattern that is predicted to correspond to the phenomenon of interest, but results from factors other than that phenomenon.

To illustrate this notion of unreal pattern, consider the experiment of detecting weak neutral currents. Weak neutral currents can be produced when a neutrino strikes a nucleon. During the experiment, however, the emitted neutrinos will also strike the chamber and the surrounding apparatus, producing a large number of neutrons. When these neutrons strike nucleons, they will produce a shower of hadrons, which leaves movement patterns mimicking those of the strongly interacting particles produced in weak neutral current interactions (Bogen & Woodward, 1988). In other words, it is possible to observe the kind of characteristic patterns that are predicted to appear in the presence of weak neutral currents, even when weak neutral currents do not actually occur. In this case, such patterns might be called “unreal” in the sense that although they can be identified on the bubble-chamber photographs, they fail to serve as evidence for the existence of weak neutral currents.

5. Patterns in data as targets of systematic explanation

Nature is complex, yet also full of patterns requiring explanation. In many cases, scientists search for patterns in data not because they need them as evidence for the existence of phenomena to be detected, but simply because they want to find in a messy and constantly changing world some order or feature that is worth explaining. In this research context, identifying patterns from data becomes the starting point of these scientists' research, and the attempts to provide systematic explanation for the existence of these patterns usually inspire and lead to significant theoretical development in science, such as the development of unifying, explanatory theories. In this section, I will first introduce some examples of patterns that have served as targets of systematic explanation and featured in theoretical development in science. Then I will discuss a number of desiderata for identifying real patterns in data (i.e., patterns that are qualified as targets of systematic explanation).

5.1 Examples of important patterns in nature

As mentioned above, one of the most important tasks in scientific inquiry is to identify real patterns from data, which can then serve as targets of systematic explanation. Ecology is a particularly apt discipline to focus on for the explication of this role of patterns in data because it heavily relies on bottom-up, data-driven inquiry and is fully of interesting patterns in need of explanation. These patterns usually work as the first step of many ecological studies. In his introduction to *Geographical Ecology*, ecologist Robert MacArthur (1972, p. 1) wrote: "To do science is to search for repeated patterns, not

simply to accumulate facts, and to do the science of geographical ecology is to search for patterns of plant and animal life that can be put on a map." Ecologist John Lawton (1996, p. 145) even claimed that "[w]ithout bold, regular patterns in nature, ecologists do not have anything very interesting to explain". In the following, I will introduce some examples of ecologically significant patterns and explain why they have garnered the attention of ecologists.

The species-area relationship

The species-area relationship is one of the most well-established patterns in ecology. It says that species number in an area tends to increase along with the area sampled in a region with a relatively uniform climate. This general pattern has been identified across a variety of taxonomic groups, ecosystems, and climate zones. Ecologist Thomas Schoener (1976, p. 629) even described it as "one of community ecology's few genuine laws." The species-area relationship is best documented in studies on island-like habitats such as actual islands, lakes, mountaintops, and springs. Compared with other kinds of habitats, these insular habitats have well-defined boundaries and are hence easier to study.

The species-area relationship has played a very important role in the development of some ecological theories by serving as a robust pattern that invites explanation. In their seminal book *The Theory of Island Biogeography*, MacArthur and Wilson (1967, p. 8) say, "Theories, like islands, are often reached by stepping stones. The 'species-area' curves are such stepping stones." In fact, one of the major motivations for them to develop their equilibrium theory of island biogeography, which later became a seminal

work in biogeography and ecology, is to explain the species-area relationship exhibited on different-sized islands.

The checkerboard distribution pattern

Species occurrence sometimes demonstrates very intriguing patterns. The knob-billed fruit dove (*Ptilinopus insolitus*) and the claret-breasted fruit dove (*Ptilinopus viridis*) belong to the same genus *Ptilinopus*. They are ecologically similar in the sense that both live in similar habitats (forest canopies) and eat similar food (fruit). Their distribution ranges on New Guinea and nearby islands are shown in Figure 1-4 respectively.

(A) *Ptilinopus insolitus* (B) *Ptilinopus viridis*

Figure 1-4. The distribution ranges of two species of fruit doves
(the maps were downloaded from BirdLife Data Zone http://datazone.birdlife.org)

There are two salient features of their joint distribution pattern. First, the range of *Ptilinopus viridis* encompasses that of *Ptilinopus insolitus*. Second, these two species do not co-occur except on one island. This pattern, called *checkerboard distribution* because

the ranges of two species interlace like black and white squares on a checkerboard, has garnered great attention from ecologists. Some ecologists, such as Diamond (1975), believe that the existence of such checkerboard distribution patterns is mainly the result of interspecific competition for limited resources. By contrast, Connor and Simberloff (1979) contend that this pattern might just be a result of random assembling or can be expected by chance alone, and they argue that a "null model" based on a randomization procedure needs to be constructed to test this hypothesis. Although the debate was initially about how to explain the formation of checkerboard distribution patterns, it has kindled a more general discussion on the usefulness of null models in biology (Connor & Simberloff, 1983, 1984; Gilpin & Diamond, 1982, 1984; Gotelli & Graves, 1996).

Patterns of relative species abundance

Relative species abundance (RSA) describes how common or rare a species is compared with other species in an ecological community. Ecologists usually start with sampling species in a target ecological community and then count the number of individuals for each species in the sample. RSA can be presented in several different ways, one of which is to use Preston's (1948) plot. The x-axis of this plot corresponds to *abundance class*, which is typically the number of individuals per species (1, 2, 3, …). Preston, however, uses aggregated abundance classes called *octaves* (1-2, 2-4, 4-8, …), which are ranges of the number of individuals per species. The y-axis corresponds to the number of species per octave. For example, in Figure 1-5, the first data-point corresponds to the octave 1-2 and its value on the y-axis is about 22. This means that 22 species in this sample have one

or two individuals[2]. Preston (1948) found that the RSA in many ecological communities follows a lognormal distribution when data are processed in his way.

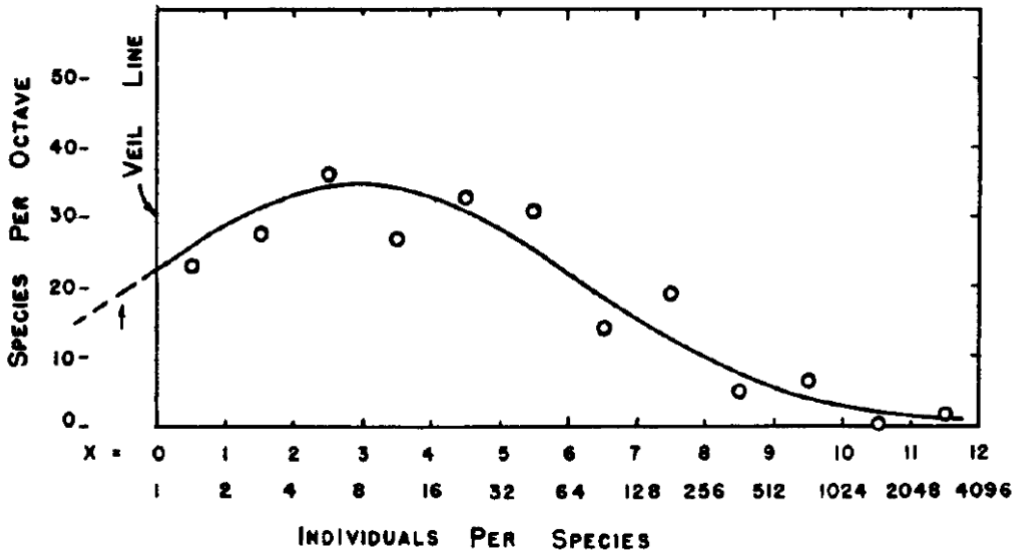


Figure 1-5. Preston's (1948) reanalysis of the RSA of moths collected by C.B. Williams

Some biologists believe that there can be a general theoretical explanation for the existence of such patterns, and they have proposed various theories in order to achieve this goal. For example, Stephen Hubbell (2001) developed a neutral theory of biodiversity by assuming that ecological communities are structured entirely by ecological drift, random migration, and random speciation. One of the central goals of his theory is to provide a general framework for accurately predicting or explaining the relative abundance patterns of species on the same trophic level.

[2] A species falling on the boundary of two octaves contributes 0.5 to each octave.

5.2 Desiderata for identifying real patterns in data

Patterns in data can be regarded as targets of systematic explanation (i.e., are real) when they reveal some stable features of the target systems that scientists want to learn about. In contrast, there are also patterns in data that are unreal in sense of being unqualified to serve as candidates for systematic explanation. Although there are paradigm cases for both real and unreal patterns, there are no criteria that can be used to draw hard and fast distinction between these two groups of patterns. The lack of such criteria, however, does not mean that there is no distinction at all. In the following, I will specify a number of desiderata for identifying real patterns in data. These desiderata do not provide clear-cut sufficient and necessary conditions for identifying real patterns in data, but they point out important aspects that should be considered when evaluating the reality of a pattern.

Low noise level

The first desideratum is low noise level. "Noise" here refers to the discrepancy between a given pattern and the data from which the pattern is identified. How the noise level associated with a pattern in a data set is measured depends on the specific from of that pattern. For example, in the case of a checkerboard distribution pattern of two species in an archipelago, the noise level is measured by counting the islands where the two species co-occur. In the case of patterns of relative species abundance, however, the noise level can be measured by calculating the mean squared error of species abundance, which is the average squared difference between the estimated species abundance according to the proposed distribution pattern and the species abundance shown by the empirical data. No

matter how the noise level associated with a pattern is measured, other things being equal, the lower the noise level is, the more real the pattern is to researchers.

Reproducibility

Low noise level cannot be the *only* desideratum of real patterns. A pattern according in every detail with a data set is exhibited with zero noise, but it can hardly be a real pattern. This is because such a pattern is overwhelmingly determined by the idiosyncratic features of a particular data set; when it is applied to a new data set collected from a similar or even the same system, the corresponding noise level will be extremely high. This fact tells us that it is inappropriate to evaluate the reality of a pattern by merely considering its corresponding noise level in one data set. Rather, a real patten is expected to be exhibited with allowable noise level in *different* empirical data sets about the same system or similar systems. Call this desideratum the *reproducibility* of patterns in data. According to this desideratum, when a pattern is exhibited with zero (or extremely low) noise level in only one or very few data sets but with extremely high noise level in most other data sets collected from the same system or similar systems, it is unsuitable to be taken as a real pattern for systematic explanation.

A real pattern is intended to reveal features or order of its target system in the *real world*, not merely the formal properties of data. Low noise level and reproducibility are two important features of real patterns, but these two features alone are not enough to guarantee the realness of a pattern because they only concern the *formal* properties of data sets. To evaluate the realness of a pattern, we should also consider the way the

relevant data are collected from the target system and the way they are classified and processed in order to identify the pattern.

Representative sampling

To detect real patterns in a target system, the ideal is to make a complete census of every relevant entity in that system and collect data from each of them. While sometimes this is possible, in most cases it is impractical. In actual processes of pattern-seeking, scientists usually have to rely on the data collected from a sample of the target system, and the goal is to be able to understand the target system through the sample, or, in Preston's (1948, p. 254) words, to "deduce the '*universe*' from the *sample*."

In order to achieve this goal, the sample must be *representative* of the target system with respect to the features that researchers want to know about. Call this desideratum *representative sampling*. Representative sampling should be understood as an ideal, which is a goal governing the whole sampling process and whose realization can come in degrees.

One way to improve the representativeness of a sample is to make sure that it is a random collection. Preston (1948) stressed the importance of random sampling when he discussed the study of relative species abundance of moths:

> "[I]t is important to recognize that the randomness we seek is merely randomness *with respect to commonness or rarity*. A light trap is satisfactory in this respect and samples its own universe appropriately. It is definitely *selective* in respect of phototropism, but it is *random* in respect of commonness, i.e., it does not care which of two moths, equally phototropic, it catches, though one may be a great rarity and the other of a very common species." (p. 254)

Preston thinks that although sampling moths with a light trap is selective with respect to phototropism, it is random with respect to the commonness of different moths. This is not necessarily true because moths of different species may have different levels of phototropism, which will bias the relative abundance of different species of moths in the sample. For example, if moths of a very rare species are more likely to be attracted by light, this species of moths would be more common in the sample than in the actual community. As I mentioned earlier, the representativeness of a sample can come in degrees. The more biased the sample is, the less likely it is for researchers to identify real patterns in the target system.

Good scientific classification

Good scientific classification is essential for identifying real patterns from empirical data sets. In Section 5.1, I introduced three important patterns that ecologists take to be real and worthy of systematic explanation, each of which involves the use of *species* as a kind to classify the organisms in their respective target systems: The species-area relationship concerns the number of species in a given area; the checkerboard distribution pattern involves the geographic locations of species; the pattern of relative species abundance concerns the number of individuals per species sampled in a given community. Without the use of *species* as a proper scientific kind, it is even impossible for ecologists to identify and formulate these patterns.

A real pattern that is qualified as a target of systematic explanation should be a pattern based on good scientific classification and involving the use of *proper scientific kinds* or *real kinds*. There are various philosophical accounts of what counts as a real kind,

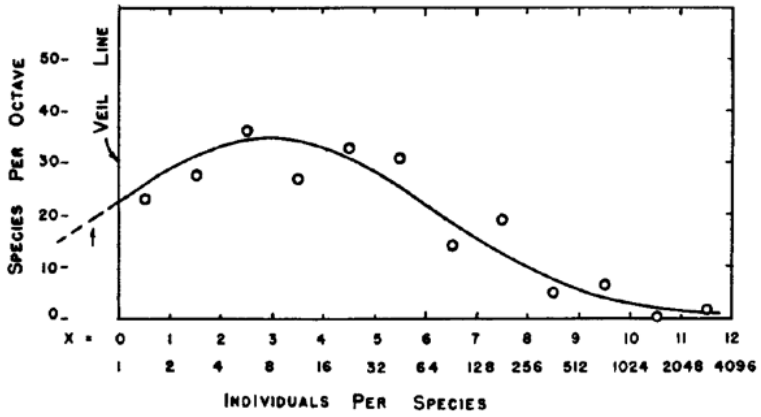
and it goes beyond the scope of this chapter to come with a new one. But for a good example of such a theory, consider briefly Quayshawn Spencer's (2012, 2016) genuine kind theory. According to Spencer (2012, p. 181), a genuine kind is "a valid kind in a well-ordered scientific research program." Here a well-ordered scientific research program (SRP) refers to a SRP that is organized to achieve long-term scientific progress. A valid kind in such a SRP is a kind that is both epistemically useful and epistemically justified in that SRP (for more details of this theory, see Spencer (2012, 2016)).

Proper data processing

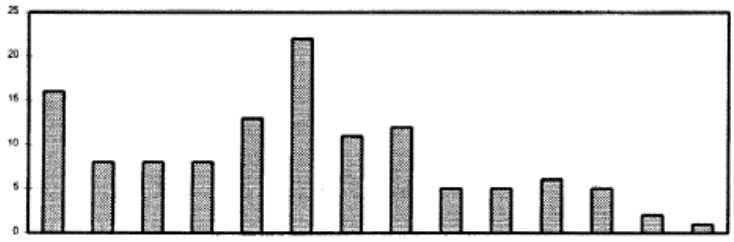
Patterns are not always immediately discernible in raw data. In many cases, researchers need to process the raw data in a certain way in order to discern the pattern. But at the same time, improper data processing may lead to the production of unreal patterns.

In Section 5.1, I introduced how to use Preston's (1948) *octaves* to plot distribution patterns of relative species abundance. When Preston's octaves are not used, the x-axis on a plot of relative species abundance corresponds to the number of individuals per species (1, 2, 3, …), and the y-axis corresponds to the number of species having a certain number of individuals. On such a plot, data points tend to be dense at the end of rare species and sparse at the end of common species, which makes it difficult to discern a pattern for the overall distribution of relative species abundance. To avoid this problem, Preston uses aggregated abundance classes called *octaves* (1-2, 2-4, 4-8, …) on the x-axis, which are ranges of the number of individuals per species. For example, the first octave (1-2) includes species having 1 or 2 individuals in the sample, and the number of species belonging to this octave should be summed up together as one data point. If a

species falls on the boundary of two octaves, it contributes 0.5 to each octave. For example, if 5 species are found to have 2 individuals in the sample respectively, they together should contribute 2.5 species to the 1-2 octave and 2.5 to the 2-4 octave. Adopting this kind of logarithmic scale for the x-axis allows Preston to display data points spanning over a wide range of values in a more compact way, which facilitates his identification of the lognormal distribution pattern of relative species abundance in many ecological communities (see Figure 1-6 (a) for an example of such a distribution pattern).



(a) Lognormal distribution of relative species abundance in a moth community according to Preston's method of octave construction, from Preston (1948)



(b) Bimodal distribution of relative species abundance in a dung beetle community according to an erroneous method of octave construction, from Lobo and Favila (1999)

Figure 1-6. Distribution patterns of relative species abundance according to two different methods of octaves construction.

Preston's method of octave construction has been widely used by ecologists to process data on relative species abundance, but sometimes it is used mistakenly, which leads to the identification of unreal patterns in data. For example, according to Preston's method, species falling on the left boundary of the 1-2 octave (i.e., species having one individual in the sample) should contribute only half of its number to this octave. However, some ecologists forgot this rule and included all the species with one individual to the 1-2 octave, leading to an increase of the number of species in the first octave. Instead of identifying a lognormal distribution as shown in Figure 1-6 (a), they found a bimodal distribution as shown in Figure 1-6 (b). This bimodal distribution should not be regarded as a real pattern exhibited by the data on relative species abundance. Rather, it is a statistical artifact resulting from researchers' improper data processing.

6. McAllister's stipulationist view of physically significant patterns in data

After introducing the pragmatic approach to the reality of patterns in data, I now turn to a different account of patterns in data advocated by James McAllister (1997, 2010), which I call the *stipulationist* view.

McAllister starts by asking a question as follows: Mathematically speaking, any empirical data set can be said to exhibit infinitely many possible patterns with various noise levels. If we accept the distinction between data and phenomena as advanced by Bogen and Woodward, and if we believe that only some of the infinitely many possible patterns exhibited by a data set correspond to phenomena in the world, then how could we distinguish between patterns that correspond to phenomena and patterns that do not? Since McAllister (2010) defines a pattern that corresponds to a structure in the world (i.e.,

a phenomenon) as being *physically significant*, the above question can also be phrased as follows: How could we distinguish between physically significant and insignificant patterns?

McAllister (2010) sets two restrictions on possible answers to this question. First, the distinction between physically significant and insignificant patterns should not be based on our knowledge, beliefs, expectations, or assumptions about what phenomena there are in the world. The reason, according to McAllister, is that we are supposed to infer the existence of phenomena in the world by identifying physically significant patterns in data, not the other way around. Second, the distinction between physically significant and insignificant patterns can only appeal to *intrinsic* facts about patterns themselves. Contingent facts such as human preferences should not be used as the criterion.

Under these two constraints, McAllister denies the possibility of specifying a respect in which physically significant patterns differ from physically insignificant patterns in empirical data sets. In particular, he rejects the view that physically significant patterns should be patterns with low noise level.

To illustrate this point, he considers the research on the speed of rotation of the Earth. The rotation rate of the Earth is not constant, which leads to variations in the length-of-day (LOD). By analyzing the empirical data about the length-of-day, geophysicists have identified multiple patterns. These include a linear increase in the LOD of about 1 to 2 milliseconds per century; a pattern with an amplitude of a few milliseconds and a period of around a decade; a fluctuation with an amplitude of around 0.2 milliseconds and a period of between 40 and 50 days; and several fluctuations with

amplitudes of around 0.1 milliseconds and periods of a few days. Among these patterns, the last pattern – fluctuations with amplitudes of around 0.1 milliseconds and periods of a few days – only accounts for about 1% of the overall variation of the LOD data. According to McAllister's interpretation, when geophysicists pick out such a pattern, they regard 99% of the variation of the LOD data as noise. He uses this example to show that patterns with high noise level can also be regarded as physically significant by scientists. Hence, low noise level cannot be used as an overarching criterion for distinguishing between physically significant and insignificant patterns (McAllister, 2010).

After failing to identify a respect in which physically significant patterns differ from physically insignificant ones, McAllister suggests that we regard all patterns exhibited by empirical data sets as physically significant. According to this view, some patterns are picked out by researchers and regarded as corresponding to phenomena, not because they have some inherent features that distinguish them from other patterns, but because they happen to be the patterns that researchers intend to study or to explain. In other words, according to McAllister, "which patterns count as those corresponding to phenomena is entirely a matter of stipulation by investigators" (McAllister, 1997, p. 224), and "any of the infinitely many patterns that data sets exhibit may be taken as the explananda of scientific theories" (p. 227).

7. Problems of the stipulationist view through the lens of the pragmatic approach

One fundamental issue with McAllister's stipulationist view is that he fails to distinguish clearly between two different roles of patterns in data in scientific inquiry. Sometimes he

describes patterns in data as corresponding to and constituting evidence for phenomena in the world, while sometimes he treats patterns in data as the explananda of scientific theories. As I have argued in previous sections, serving as evidence for the existence of scientific phenomena and as candidates for systematic explanation should be understood as two different roles that patterns in data are expected to play in scientific inquiry. Researchers are faced with different issues when utilizing patterns in these two different ways.

Let's first analyze the case where patterns in data are expected to provide evidence for the existence of scientific phenomena. According to McAllister, the question at issue is how to distinguish patterns that correspond to phenomena (i.e., physically significant patterns) from patterns that do not. Call it the *demarcation question of physically significant patterns*. Instead of focusing on a specific pattern in data and determining whether it corresponds to the phenomenon of interest, the demarcation question of physically significant patterns demands an *overarching* criterion that can be used to evaluate the physical significance of all the possible patterns exhibited by a data set. Framing the question at issue in this way, however, is misleading in the context of phenomenon detection. When seeking evidence for the existence of a phenomenon, researchers need *not* answer the demarcation question of physically significant patterns as suggested by McAllister. Instead, they should consider the following three questions:

> (i) Given the phenomenon under investigation and the detection method employed, what kind of pattern is expected to be exhibited by the relevant data if the phenomenon under investigation indeed exists?
>
> (ii) To what extent is the expected pattern exhibited by the relevant data?

(iii) Do the relevant data exhibit the expected pattern to a great enough extent so that they can serve as evidence for the existence of the phenomenon under investigation?

Given these questions, we can see that although any empirical data set can be described as infinitely many possible patterns with various noise levels, only the pattern that is predicted to correspond to the phenomenon of interest is relevant in the context of phenomenon detection. The determination of this pattern is not a matter of stipulation, but based on researchers' proposed hypothesis about the phenomenon of interest, knowledge about the experimental setting designed to detect the phenomenon, and other non-arbitrary background assumptions. As for the other possible patterns in the data set, they may either correspond to phenomena that are not the focus of the current study or have no clear physical meaning at all, and neither of these two types of patterns is relevant for the research purpose. Hence, researchers do not need to come up with an overarching criterion to demarcate patterns that correspond to phenomena and patterns that do not. They only need to focus on the pattern that is predicted to correspond to the phenomenon of interest.

To illustrate my point, consider first the example of determining the melting point of lead. If lead really has a fixed melting point under certain environmental conditions, then given certain assumptions (e.g., there is no systematic error introduced by the equipment), the measurement results would be expected to follow a normal distribution. The determination of this characteristic pattern does not depend on stipulations by investigators, but on the proposed property of the phenomenon to be detected (the fixedness of the melting point of lead) and a series of empirical assumptions about the experimental conditions. Researchers need to evaluate the degree to which the

measurement results follow a normal distribution pattern through statistical analysis and decide, based on the statistical analysis results, whether the data can support the claim that lead has a fixed melting point under certain environmental conditions. It is irrelevant for their purpose whether the other infinitely many patterns exhibited by the data set can serve as evidence for other potentially existing phenomena.

The same point can also be illustrated with the example of detecting weak neutral currents. Weak neutral currents occur in a variety of interactions involving the weak force. For example, the Weinberg-Salam theory predicts that weak neutral currents will be produced when a neutrino strikes a nucleon. Such an interaction will produce a set of strongly interacting particles, leaving certain characteristic tracks (i.e., movement patterns) while moving through a bubble chamber. In this case, seeking evidence for the existence of weak neutral currents amounts to looking for bubble-chamber photographs with particle movement patterns of a particular kind. The determination of this kind of movement pattern does not rely on researchers' stipulations, but on the proposed properties of weak neutral currents, the researchers' knowledge about the experimental setting, as well as other experimental and theoretical assumptions. Bubble-chamber photographs may also exhibit other kinds of movement patterns, which may even indicate the occurrence of interactions other than weak neutral currents. But insofar as the goal of researchers is to detect weak neutral currents, the physical significance of these movement patterns is irrelevant in the current research context.

Now let us address some concerns that proponents of McAllister's view might raise. First, according to my account, researchers need to determine what kind of pattern corresponds to the phenomenon of interest given a certain detection method. Doesn't this

amount to answering McAllister's demarcation question of physically significant patterns? One way to determine whether two questions are essentially the same is to look at the kind of answer that is expected for each question. To answer McAllister's demarcation question, the researcher needs to come up with a criterion that can be used to determine whether each of the infinitely many possible patterns in a data set corresponds to a phenomenon in the world, no matter what that phenomenon is. By contrast, to answer "What kind of pattern is expected to be exhibited by data if the phenomenon of interest exists?", the researcher only needs to focus on a particular phenomenon and predict *one* kind of characteristic pattern that corresponds to the focal phenomenon; the researcher's answer to the above question cannot help determine whether other patterns exhibited by the same data set correspond to phenomena or not. Hence, the research question about patterns in data asked in the context of phenomenon detection is different from McAllister's demarcation question.

Second, if the characteristic pattern that is predicted to correspond to a phenomenon of interest is partly determined by the presupposed properties of that phenomenon, how could such a pattern serve as evidence for the existence of the phenomenon? Isn't there a problem of circularity? This problem does not really exist, because there is no *a priori* guarantee that the expected pattern will be exhibited by the data set with a high enough degree. For example, in the case of determining the melting point of lead, the thermometer readings may show a poor fit with the expected normal distribution; in the case of detecting weak neutral currents, the bubble-chamber photographs may not show the kind of movement patterns that are expected to appear as a result of weak neutral currents. Since the evidential relationship between patterns in

data and phenomena is an empirical rather than *a priori* relationship, the worry of circularity is unfounded.

I have responded to McAllister's stipulationist view of physically significant patterns in data by considering the case where patterns in data are expected to serve as evidence for the existence of scientific phenomena. I now turn to the case where patterns in data serve as targets for systematic explanation. In this context, McAllister's demarcation question becomes relevant, but it should be reformulated in a way to match the role of patterns under consideration. Instead of asking "How to distinguish patterns that correspond to phenomena from patterns that do not?", the relevant question is:

> How to distinguish patterns that can serve as targets for systematic explanation from those that cannot?

As I emphasized in Section 5.2, although there is no *hard and fast* distinction between these two classes of patterns, it does not mean that there is no distinction at all. In Section 5.2, I have specified a number of desiderata that can be used to evaluate whether a pattern in data can serve as a target of systematic explanation. Hence, it is wrong to claim that "any of the infinitely many patterns that data sets exhibit may be taken as the explananda of scientific theories" (McAllister, 1997, p. 227).

In particular, I want to argue against McAllister's denial of low noise level as a feature of patterns that deserve systematic explanation. As is evident in his discussion about patterns in the length-of-day data, when an empirical data set contains multiple superimposed patterns, the noise of any single pattern, according to McAllister, amounts to the sum of all the other patterns and a further residual noise term. This calculation of the noise level of a pattern, however, ignores the fact that different patterns identified

from the same data set are on different scales and capture features regarding different aspects of the data. Given this fact, the noise associated with one pattern may not count as noise for another. For example, one pattern identified by geophysicists from the length-of-day data says that the length-of-day increases by 1 to 2 milliseconds per century. Since this pattern concerns the increase of the length-of-day on the time scale of a century, variations of the length-of-day on other time scales should not count as noise for this pattern. By the same token, fluctuation patterns identified on other time scales should not be regarded as noise associated with this pattern, either. When calculated this way, the noise level attributed to patterns identified by geophysicists from the length-of-day data would drop dramatically. Although it is up to researchers to determine the highest acceptable noise level, they tend to set the threshold value at a relatively low noise level. In other words, low noise level is indeed a desideratum of real patterns.

8. Conclusion

In this chapter, I have endeavored to show that patterns in data can play three different epistemic roles in scientific inquiry. Accordingly, the realness of a pattern identified from data should be evaluated based on the extent to which it fulfills the epistemic role that it is expected to play in a specific research context. There is no single, over-arching account of real patterns. I have also argued against McAllister's stipulationist view of patterns in data and shown that whether a pattern corresponds to a phenomenon in the world, or whether a pattern can be regarded as a target of systematic explanation, is not a matter of stipulation by investigators.

Chapter 2: The use and limitations of null-model-based hypothesis testing

1. Introduction

In a study of bird communities on New Guinea and nearby islands, especially the Bismarck Archipelago, Diamond (1975) claimed to have found certain "assembly rules" with respect to the distribution of bird species. One of them says that "[s]ome pairs of species never coexist, either by themselves or as part of a larger combination" (Diamond, 1975, p. 344). For example, the Mackinlay's cuckoo-dove (*Macropygia mackinlayi*) and the bar-tailed cuckoo-dove (*Macropygia nigrirostris*), while ecologically similar and overlapping in their geographical ranges, never co-occur on any island of the Bismarck Archipelago.[3] This pattern, called by Diamond a "checkerboard distribution" because the geographical ranges of the two species interlace like black and white squares on a checkerboard, seems to require an explanation.

Diamond (1975) proposed the hypothesis that the existence of such checkerboard distribution patterns can be explained by, among other things, interspecific competition for limited resources. Some other ecologists, however, thought that it is premature to infer the existence of competitive exclusion among relevant species just by looking at their distribution patterns. For example, Connor and Simberloff (1979) argued that in order to demonstrate that competition is responsible for the formation of checkerboard distribution patterns, one needs to first falsify a null hypothesis that those patterns are due

[3] In species co-occurrence studies, when claiming that a species exists, occurs, or is present on an island, ecologists typically mean that the species has established a breeding population on that island instead of just having several vagile individuals.

to the random colonization of bird species. Their strategy is to build a null model in which bird species are randomly assigned to different islands of an archipelago under certain constraints and then calculate the values of certain statistics such as the number of species pairs that never co-exist on any island. If the expected number of forbidden pairs (or the value of other chosen statistics) is not statistically significantly different from what is obtained based on the empirical data collected from the actual archipelago, then there is no strong reason to appeal to interspecific competition as the explanation of checkerboard distributions.

Connor and Simberloff's challenge triggered sharp rebuttals from Diamond and his colleagues (e.g., Diamond and Gilpin, 1982; Gilpin and Diamond, 1984), which in turn incurred further rejoinders from Simberloff and his colleagues (e.g., Connor and Simberloff, 1983, 1984). This disagreement has led to a schism between two camps that persists even today (for a recent round of debate, see Connor et al., 2013, 2015; Diamond et al., 2015).

This debate is worth attention because the strategy used by Simberloff and his colleagues, which I will call *null-model-based hypothesis testing*, has been widely used in the biological sciences, especially in ecological research such as studies of species co-occurrences, species/genus (S/G) ratios, food webs, and character displacement. To be clear, the use of the term "null model" is somewhat inconsistent in the biological literature. For example, Hubbell (2001) and Rosindell et al. (2011) argue that the neutral model of biodiversity provides a useful null model in community ecology, in which the term "null model" just means a model providing a null hypothesis. While the practice of using the neutral model as a null model has been criticized by Bausman (2018), the

neutral model that he considers is different from the null model that I will focus on here.[4] The kind of null model that I will consider in this chapter is also called "random model" or "stochastic model," which is constructed based on a *randomization* procedure and used to test the hypothesis that the existence of a pattern is the result of random processes or can be expected by chance alone. This type of model is regarded by its proponents as playing a role similar to the "control" as used in traditional statistical hypothesis testing in experimental settings, and it is said to provide a null hypothesis against which other hypotheses should be tested.

At the heart of the debate concerning null models is whether null hypotheses and null models are useful at all in the biological sciences. Since an appropriate null model is essential for the validity of null-model-based hypothesis testing, most discussions have been focused on whether it is possible (and if so, how) to construct a model that is genuinely null. Many constructive discussions have taken place, but many technical details remain controversial. This chapter contributes to the literature from a somewhat different perspective. Assuming that the technical controversies about the construction of null models can be resolved, what would be the possible use of null-model-based hypothesis testing, if it is useful at all, and how could that use be justified? What limitations does this strategy have? These are the questions that I aim to answer in this chapter.

My strategy is to use as an example the controversy over Connor and Simberloff's advocacy of null hypotheses and null models in species co-occurrence studies and draw

[4] For a detailed discussion of the differences between neutral models and null models, see Gotelli and McGill (2006).

some general lessons from it. I will argue that null-model-based hypothesis testing as a research strategy can be useful – but in a limited sense. It is useful not because it works as an analog or approximation to traditional statistical hypothesis testing in well-controlled experimental settings, but because it provides a possible way to challenge scientists' commonsense judgments about how a seemingly unusual pattern could have come to be. To better demonstrate this point, I will compare the null model used by Connor and Simberloff with Schelling's model of segregation. I will also analyze the limitations on the use of null models and discuss some lessons drawn from the debate concerning the use of null-model-based hypothesis testing in species co-occurrence studies.

2. Null-model-based hypothesis testing in species co-occurrence studies

In order to answer the general question of the use and limitations of null-model-based hypothesis testing, it is necessary to properly detail how it is actually used in scientific research. In this section, I will use Connor and Simberloff's (1979) null model of species co-occurrences as a representative example to illustrate how null-model-based hypothesis testing has been employed as a research strategy in the biological sciences.[5]

[5] In species co-occurrence studies, the null models constructed by different ecologists may be more or less different from each other. Even Connor and Simberloff themselves keep modifying their null models in later publications. Nevertheless, the version I will introduce here, which appears in one of their earliest and also most-cited publications on this subject, helps demonstrate the key features of null-model-based hypothesis testing.

2.1 Constructing the null model

Table 2-1. A 3-by-4 random matrix

	Island A	Island B	Island C	Island D	Row sum
Species a	1	0	1	0	2
Species b	1	0	0	1	2
Species c	0	1	0	1	2
Column sum	2	1	1	2	

Connor and Simberloff (1979) want to use their null model to construct a simulated archipelago in which bird species are randomly assigned to the islands. The null model used in their species co-occurrence analyses is actually a set of *random matrices*. In the rest of this section I will proceed by explaining what a random matrix is, how to construct it, and in what sense it is "random."

A random matrix used in species co-occurrence analyses is a rectangular array of 1's and 0's, in which each row corresponds to a species, and each column an island within an archipelago (see Table 2-1). The number "1" means that a species is present on an island, while "0" means that a species is absent. Hence, the process of randomly assigning species to islands can be simulated by the process of randomly placing 1's and 0's in a matrix.

Since each element in the matrix has two choices (1 or 0), for a matrix with m rows and n columns, there will be 2^{mn} unique matrices if there is no constraint about how to place 1's and 0's, which correspond to 2^{mn} different ways of distributing m species on

n islands. But in the relevant literature, the placement of species on islands in a random matrix is almost always subject to some constraints. Connor and Simberloff (1979, p. 1133) use the following three constraints:

> (i) For each island, there is a fixed number of species, namely, that which is observed.
> (ii) For each species, there is a fixed number of occurrences, namely, that which is observed.
> (iii) Each species is placed only on islands with species numbers in the range for islands which that species is, in fact, observed to inhabit. That is, the "incidence" range convention is maintained.

The first constraint requires that each island hold a fixed number of species, which is equal to the number of species actually observed on each island. For example, if a real island holds two bird species, it should also hold two in the random matrix. Since a column sum in a random matrix corresponds to the number of species present on an island, constraint (i) is equivalent to keeping all the column sums fixed at certain numbers according to the number of species actually observed on each island. Similarly, constraint (ii) requires that each species occur on a fixed number of islands, which is equivalent to keeping all the row sums fixed at certain numbers according to the number of islands on which each species actually occurs. The third constraint is more complicated. Some species may occur on islands with a wide range of species numbers, while some others may be present only on species-poor (or, conversely, species-rich) islands. Hence, constraint (iii) is a further restriction on the kind of islands to which each species can be assigned. Note that although the matrices are called by Connor and Simberloff as "random matrices," the constraints used in these matrices are not themselves random. Rather, they are decided according to the empirical data collected from the actual archipelago. From a statistical point of view, these constraints amount to

very strong parametric restrictions. The matrices are called "random" because Connor and Simberloff randomize the placement of bird species on islands in the simulation given the preset constraints. Accordingly, a distribution pattern is said to be generated by the species randomly colonizing an archipelago if their colonization of islands is not subject to any other constraints besides the ones already mentioned above.

If all the non-equivalent random matrices satisfying the preset constraints are collected together, they form the *full null space*. Given the number of species and islands in an actual archipelago (e.g., there are at least 147 species of land birds and 50 islands in the Bismarck Archipelago), the number of random matrices in this space can be very large. When it is computationally intractable to get all the possible random matrices, one can collect a sample of them. Random matrices in this sample constitute the *sample null space* (see Figure 2-1).

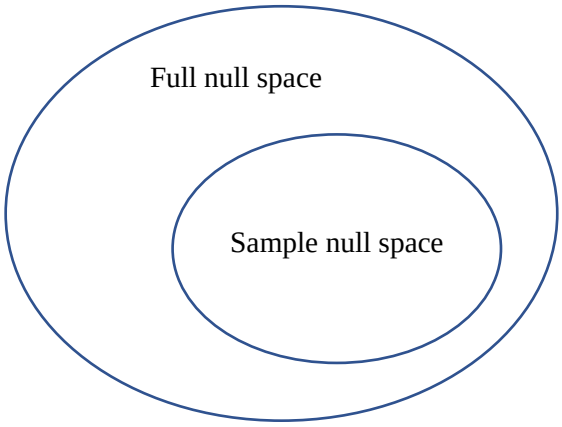


Figure 2-1. The relationship between the full null space and the sample null space

2.2 Comparing simulated data with empirical data

The test is conducted by comparing the empirical data collected from the actual archipelago with the simulated data generated by the null model. In order to conduct this test, one first needs to choose a statistic (i.e., a measure of some attribute of the sample) so that it can be used to make the comparison. There is more than one kind of statistic that can be used for the comparison, but what is most directly relevant to checkerboard distributions is the number of pairs of species that never co-occur on any island within an archipelago.

When understanding each random matrix in the sample null space as a simulated archipelago, one can count how many pairs of non-coexisting bird species there are on each of those archipelagos. Since these numbers may not be exactly the same, what one actually obtains is a *null distribution*, which describes the probabilities of all the expected values of the number of non-coexisting pairs based on the null model. Once this distribution is obtained, one can calculate its mean and standard deviation, compare them with the number of non-coexisting species pairs in the actual archipelago, and see whether there is a statistically significant difference between them. If no such difference is found, it means that the existence of checkerboard distributions is consistent with the result of random colonization. If so, Connor and Simberloff (1979) argue, then there is no strong reason to appeal to interspecific competition as the explanation of checkerboard distributions. It is worth noting that depending on the target phenomena and statistics of interest, researchers may choose measures other than the means and standard deviations of null distributions to conduct the test.

2.3 Technical controversies concerning the test

Many discussions have taken place concerning Connor and Simberloff's null model. Diamond and Gilpin (1982), for example, provide seven criticisms of Connor and Simberloff's (1979) approach. Here I only recapitulate two issues that have drawn the most attention. The first problem is called the *dilution effect*. According to Diamond and Gilpin, interspecific competition most likely happens within guilds, i.e., groups of ecologically similar species overlapping in resource utilization. Connor and Simberloff, however, conduct their test in whole faunas. As a result, the effects of interspecific competition within guilds are diluted by a mass of irrelevant data from ecologically distinct species. But this should be understood as a criticism of the specific model constructed by Connor and Simberloff (1979), rather than the use of null models as a whole. In fact, Simberloff and his colleagues have accepted this criticism and revised their models accordingly in later publications (Connor et al., 2013).

Another, perhaps more serious, problem is the incorporation of *hidden effects of competition* into the null model. In Connor and Simberloff's random matrices, the placement of species on islands is subject to three constraints. Diamond and Gilpin argue that since constraints (ii) and (iii) are themselves strongly influenced by competition, a null model subject to these constraints would already contain some effects of competition in its structure, making the model not as "null" as it needs to be. Since the construction of a null model always involves some constraints, the problem always exists that some effects of competition have already been included in the null model. If this is true, it would be a criticism of the use of null models as a whole, at least in studies of species co-occurrences. But whether this is a fatal issue is still controversial.

Technical issues like these, although important, are not the focus of this chapter.[6] In what follows, I will put aside these technical issues for a moment and consider instead some more general questions about the use and limitations of null-model-based hypothesis testing as a research strategy in the biological sciences. The benefit of doing so is that it can deepen our understanding of this research strategy in a more general way without being trapped in still unsolved technical controversies.

3. A critical evaluation of null-model-based hypothesis testing

3.1 Connor and Simberloff's interpretation

As mentioned before, advocates of null models think that null models provide a null hypothesis against which other hypotheses should first be tested. Null-hypothesis testing is not a native research method in ecology. Instead, it is borrowed from statistics.

The term "null hypothesis" was probably first introduced by R. A. Fisher. In his seminal book *The Design of Experiments*, Fisher (1935) considered a case where a lady claimed that by tasting a cup of tea mixed with milk she could tell whether the milk or the tea was first added to the cup. He designed an experiment to test the hypothesis that the lady did not have such discrimination ability, and labelled this hypothesis as the "null hypothesis." According to Fisher, a null hypothesis like this is characteristic of all experimentation, but one may choose any hypothesis as the null hypothesis as long as it is exact and free from vagueness and ambiguity. One important feature of the null hypothesis is that it is "never proved or established, but is possibly disproved, in the

[6] For reviews of the technical issues in the construction of null models, see Gotelli and Graves 1996; Sanderson and Pimm 2015.

course of experimentation" (Fisher, 1935, p. 19). Whether the null hypothesis in an experiment should be rejected can be decided by conducting a test of significance, which was developed by Fisher in the 1920s (Fisher, 1925, 1926). The rationale behind this test is to calculate the *p*-value, i.e., the probability of obtaining a result at least as extreme as what is actually observed in the experiment given that the null hypothesis is true. If the *p*-value is smaller than a certain threshold chosen by the researcher, such as 0.05, the result of the test is said to be statistically significant and the null hypothesis is rejected.

Notice that in Fisher's tests of significance, only a single hypothesis – the null hypothesis – is considered. By contrast, in the Neyman–Pearson approach to statistical hypothesis testing, it is required that the null hypothesis be tested against an alternative hypothesis. While the debate between these two approaches is not the focus of this chapter, it is worth mentioning that the current approach to statistical hypothesis testing, which is widely used in statistical education and scientific research today, involves both the null and alternative hypotheses.

Fisher (1925, 1926, 1935) also played an important role in advocating the use of randomization in experimental design, which is used to avoid systematic biases and proves to be essential for the validity of statistical hypothesis testing in experimental research. Nowadays, randomized controlled trials[7] have become the gold standard in experimental studies, especially those that aim to test the cause-and-effect relationship between two variables. For example, in order to test whether an antihypertensive drug

[7] Although the term "randomization test" is often used interchangeably with "permutation test," actually they are different. A randomization test is based on random assignment involved in experimental design; the procedure of random assignment is conducted before empirical data are collected. By contrast, a permutation test is a nonparametric method of statistical hypothesis testing based on data resampling.

really has the effect of reducing blood pressure, subjects participating in the experiment are randomly assigned to two groups – the control group and the treatment group. Subjects in the treatment group take the drug every day, while subjects in the control group take placebo tablets, which look the same as the drug but do not contain the drug's active ingredients. Then the blood pressure data of the treatment group are compared with those of the control group statistically.

Notice that a "null model" is not needed for traditional statistical hypothesis testing used in well-controlled experimental settings (Figure 2-2a). By contrast, an appropriate null model is essential for the validity of the kind of testing conducted by Connor and Simberloff in their study of species co-occurrences – that is why I call it *null-model-based* hypothesis testing (Figure 2-2b). So the first question that we need to answer is: why is a null model needed in this kind of testing?

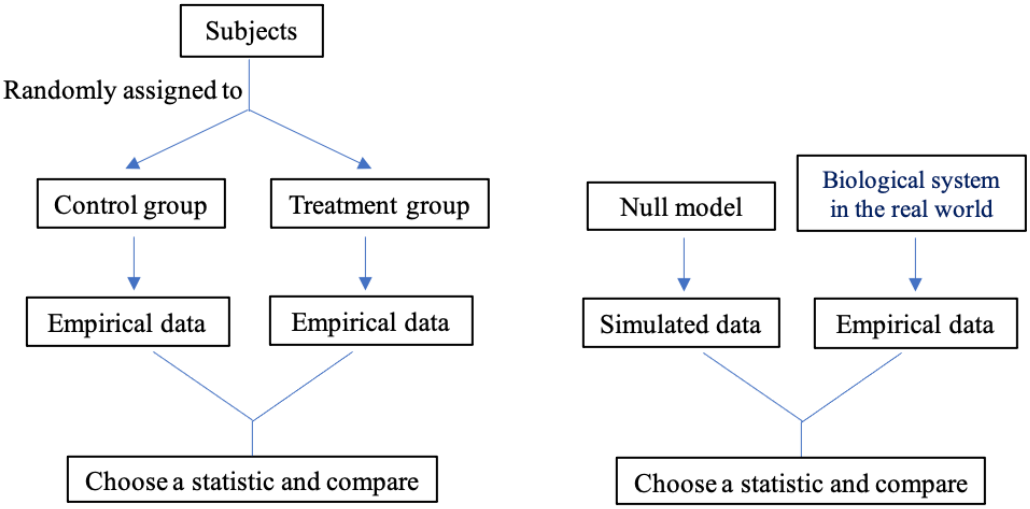


Figure 2-2. Procedures of two types of hypothesis testing

The term "null model" does not belong to the terminology of traditional statistical hypothesis testing. Instead, it was coined for the use of null hypothesis testing in non-experimental research such as many studies in ecology and biogeography. In well-controlled experimental studies, researchers collect data from both the control and treatment groups, compare two data sets with respect to a statistic of interest, and see whether there is a statistically significant difference between them. But in an ecological case, the contrast between the control and treatment groups is usually lacking. For example, in the debate about checkerboard distributions, what is of interest is whether competition is responsible for the formation of those patterns. However, it is impossible to find an actual archipelago as the "control" in which bird species are manipulated in a way such that the level of interspecific competition is set as zero.

Given this, the role of the null model, as envisioned by Connor and Simberloff (1983), is to construct an imaginary archipelago in which bird species are randomly assigned to islands within the archipelago so that the effect of interspecific competition can be excluded. By using the null model as an analog of the control in experimental research, Connor and Simberloff (1983) aim to generate *simulated data* via the null model so that they can be compared with the *empirical data* collected from the actual archipelago. If this strategy works, then null-model-based hypothesis testing seems to be justified as a legitimate extension of traditional statistical hypothesis testing.

But is this interpretation of null-model-based hypothesis testing really justified? In the following sections, I will give a critical evaluation of this interpretation.

3.2 Evaluating the interpretation

3.2.1 The mismatch problem between the null and alternative hypotheses

Traditional statistical hypothesis testing used in well-controlled experimental research involves a pair of hypotheses – a null hypothesis and an alternative hypothesis. These two hypotheses must be *mutually exclusive* and *collectively exhaustive* of all the admissible hypotheses *given the question of interest* (Sloep, 1986). For example, if researchers want to test the effect of an antihypertensive drug, then the question of interest is whether there is a cause-and-effect relationship between the use of this antihypertensive drug and the reduction of blood pressure. Given this question of interest, the null hypothesis is that such a cause-and-effect relationship holds, and the alternative hypothesis is that it doesn't. Although the reduction of blood pressure can also be caused by many other factors, hypotheses involving those factors are not admissible hypotheses given the question of interest, and hence do not undermine the "collectively exhaustive" criterion.

Now consider the null and alternative hypotheses involved in null-model-based hypothesis testing. In their widely cited paper, Connor and Simberloff (1979, p. 1132) argue that:

> In order to demonstrate that competition is responsible for the joint distributions of species, one would have to falsify a null hypothesis stating that the distributions are generated by the species randomly and individually colonizing an archipelago.

If we focus on the controversy over checkerboard distributions, it is reasonable to formulate the null (H_0) and alternative (H_1) hypotheses used in Connor and Simberloff's test as follows:

> H_0: The checkerboard distributions of certain pairs of closely related bird species on the islands of the Bismarck Archipelago are the result of random colonization.
>
> H_1: The checkerboard distributions of certain pairs of closely related bird species on the islands of the Bismarck Archipelago are caused by interspecific competition.

Before analyzing the logical relationship between these two hypotheses, it is necessary to clarify their meanings. In the interspecific competition hypothesis (H_1), competition refers to interspecific competition for limited resources, which does not include interspecific differences in dispersal abilities. As to Connor and Simberloff's null hypothesis (H_0), what exactly it means depends on one's interpretation of the null model. Gotelli and Graves (1996, pp. 3–4) provide an operational definition of a null model:

> A null model is a pattern-generating model that is based on randomization of ecological data or random sampling from a known or imagined distribution. The null model is designed with respect to some ecological or evolutionary process of interest. Certain elements of the data are held constant, and others are allowed to vary stochastically to create new assemblage patterns. The randomization is designed to produce a pattern that would be expected in the absence of a particular ecological mechanism.

This definition consists of both a *description* and an *interpretation* of a null model. The description part indicates how a null model is actually constructed: It is constructed based on the randomization of empirical data given certain constraints or random sampling from a species pool.

The interpretation part is about what a null model is intended to represent. According to the definition above, a null model in ecology is intended to simulate an ecological system where a particular ecological mechanism is excluded. Under this interpretation, Connor and Simberloff's null model is intended to simulate an archipelago

where only interspecific competition is excluded, with their null hypothesis being simply the denial of the interspecific competition hypothesis. But this interpretation faces a serious problem. As Diamond and Gilpin (1982, p. 73) rightly point out, in order to use a null model to test the effect of a particular factor, the null model must both exclude the factor to be tested and include all the other important factors that could structure the actual data. However, it is not clear how Connor and Simberloff's null model can satisfy this requirement. On the one hand, as mentioned earlier, Diamond and Gilpin (1982) argue that the constraints in Connor and Simberloff's null model contain hidden effects of competition. On the other hand, even if this problem could be somehow managed, there is no way to guarantee that all the other relevant factors are included in the null model.

Another, perhaps better, interpretation of the null model is that it is intended to provide an alternative explanation to the competing hypothesis by taking into account chance processes. Under this interpretation, Connor and Simberloff's null model is a simulation of bird species' random colonization of islands, and the constraints used in the null model are structural assumptions about the ecological system under investigation. Accordingly, their null hypothesis is an alternative explanation to, rather than a simple denial of, the interspecific competition hypothesis.

Sloep (1986, p. 309) claims that the interspecific competition hypothesis (H_1) and Connor and Simberloff's random colonization hypothesis (H_0) cannot be an appropriate pair of null and alternative hypotheses in the statistical sense because the first hypothesis does not *logically exclude* the second. This is not true. H_0 and H_1 are indeed mutually exclusive because they cannot both be true at the same time.

The real problem is that they are not *collectively exhaustive*. The question of interest in this case is how the checkboard distribution patterns have come into being. There are multiple possible answers to this question because whether two species will co-occur on the same island can be influenced by many factors other than interspecific competition, such as their dispersal abilities, habitat preferences, and responses to predators, parasites, or pathogens. Since H_0 and H_1 together do not exhaust all the admissible hypotheses given the question of interest, rejecting one of them does not necessarily provide support for the other. More specifically, rejecting that the checkerboard distribution patterns are the result of random colonization does not force us to conclude that they are caused by interspecific competition. By the same token, even if it can be shown that the patterns are not caused by interspecific competition, it does not mean that they are the result of random colonization.

My analysis above has demonstrated an important disanalogy between traditional statistical hypothesis testing and null-model-based hypothesis testing: the null and alternative hypotheses in the former satisfy the condition of being collectively exhaustive given the question of interest, while those in the latter do not. This difference is due to the fact that traditional statistical hypothesis testing and null-model-based hypothesis testing are faced with different tasks. Hypotheses involved in traditional statistical hypothesis testing are usually statements about a relationship. Since a relationship either holds or not, the "collectively exhaustive" criterion is readily satisfied. By contrast, hypotheses involved in null-model-based hypothesis testing are usually explanations of a phenomenon. Since a phenomenon usually has multiple possible explanations, the "collectively exhaustive" criterion is typically unsatisfied.

It may be argued that the mismatch problem between the null and alternative hypotheses is not a fatal issue for null-model-based hypothesis testing. For example, in the case of checkerboard distributions, one can claim that when the random colonization hypothesis (H_0) is chosen as the null hypothesis, its appropriate alternative hypothesis is *not* the interspecific competition hypothesis (H_1), but the logical negation of H_0, i.e., the hypothesis that the checkerboard distributions are *not* the result of random colonization. Let's call this updated alternative hypothesis H_1^*. As shown in Figure 2-3, while H_0 and H_1 do not satisfy the collectively exhaustive criterion, H_0 and H_1^* do.

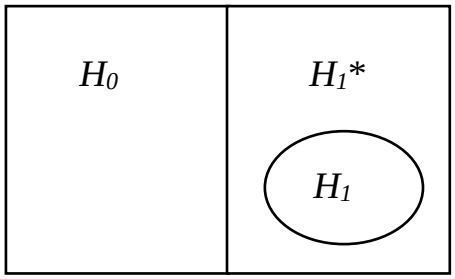


Figure 2-3. The relation between H_0, H_1, and H_1^*

Notice that the question of interest has been changed after the alternative hypothesis is reframed this way. What is of interest is no longer how the patterns have come into being, but whether those patterns are the result of random colonization. While this kind of reframing seems to circumvent the mismatch problem, it does not guarantee that null-model-based hypothesis testing is indeed an appropriate null hypothesis test in a strict statistical sense. I will explain why in the following two sections.

3.2.2 The principle of equifinality and the lack of proper control of variables

In this section, I will examine Connor and Simberloff's (1983, p. 464) claim that in null-model-based hypothesis testing, a null hypothesis and a null model are contrived to "usefully approximate the role of the 'control' in order to test a hypothesis involving non-experimental evidence," and see whether they are actually able to play the role as envisioned.

In traditional statistical hypothesis testing, what counts as a proper control group is not solely determined by the setting of the supposed control group per se, but also influenced by how the treatment group is set up. Let's again use the test of the effect of antihypertensive drugs as an example. Suppose that the subjects participating in the experiment are randomly assigned to two groups. Subjects in the supposed treatment group take the antihypertensive drug and another kind of drug every day, while subjects in the supposed control group take placebo tablets. It is clear that the supposed control group does not count as a proper control because it does not guarantee that the only independent variable in this test is whether the subjects take the antihypertensive drug or not. Without proper control of variables, one is not justified to make any causal inference about the effect of the antihypertensive drug. More specifically, one is not justified to reject the alternative hypothesis that the antihypertensive drug has the effect of reducing blood pressure even when there is no statistically significant difference between the supposed control and treatment groups with respect to the subjects' blood pressure. This is because it is possible that the antihypertensive drug is indeed effective, but the other drug has the effect of increasing blood pressure, thus counteracting its effect.

Now consider null-model-based hypothesis testing. In the last section, I have argued that there exists a mismatch between the null and alternative hypotheses commonly used in null-model-based hypothesis testing, namely, they do not satisfy the "collectively exhaustive" criterion given that the question of interest is how to explain a phenomenon. One possible way to circumvent this problem is to reframe the question of interest as whether the pattern under investigation is the result of random processes. Since the answer to this question is either yes or no, the null and alternative hypotheses after this reframing will satisfy the "collectively exhaustive" criterion. Hence, if the empirical data is consistent with the simulated data generated by the null model, one seems to be able to retain the null hypothesis and reject the alternative hypothesis, just as what researchers would do in traditional statistical hypothesis testing.

I will use the rest of this section to show that this is not the case. I argue that in null-model-based hypothesis testing, because of the lack of proper control of variables, one is not justified to reject the alternative hypothesis even when there is no statistically significant difference between the simulated and empirical data with respect to the statistics of interest. The case of checkerboard distribution patterns will still be used as an example for demonstration.

In ecology, scientists make an important distinction between *pattern* and *process* (Gotelli and Graves, 1996, p. 5). In the introduction to his book *Geographical Ecology*, MacArthur (1972, p. 1) wrote: "To do science is to search for repeated patterns, not simply to accumulate facts […]." This quote serves as a nice summary of a common approach adopted by ecologists – they start by identifying patterns in nature and then try to reveal the underlying processes that have produced these patterns. Since ecological

systems are thermodynamically open systems, the same final state may be reached from different initial states and in different ways. This has been described as the principle of equifinality (von Bertalanffy, 1968). Due to the equifinality of ecological systems, the same pattern can be produced through different (or different combinations of) processes, just as there are many roads to Rome.

In Connor and Simberloff's null model of species occurrences, bird species are randomly assigned to islands of the simulated archipelago. This procedure is intended to exclude the effects of interspecific competition, but at the same time it also ignores many other factors that may influence species' co-occurrences such as the varied dispersal abilities of different species. Hence, there is no proper control of variables in the construction of the null model. Since closely related species tend to have similar dispersal abilities, they are more likely to colonize the same islands than what they would do if they were randomly distributed, which leads to an opposite effect of interspecific competition (Colwell and Winkler, 1984; Harvey, 1987). Given the multiple producibility of patterns, the joint effects of dispersal abilities and interspecific competition may produce a similar number of pairs of non-coexisting species as would be expected by random colonization. In other words, even if the simulated data generated by the null model are not significantly different from the empirical data with respect to the number of non-coexisting species pairs, one is not justified to reject the supposed alternative hypothesis (H_1*) that the pattern is not the result of random processes.

It may be argued that if a model based on a simpler hypothesis, such as the null model based on the random colonization hypothesis in the case of checkerboard distributions, is sufficient to produce a pattern statistically indistinguishable from the

empirical pattern, then this hypothesis should be favored because of its simplicity. Although the principle of simplicity is often used to privilege simpler hypotheses over more complex ones, its use is not without controversy. For example, Sober (1988, 1994) has argued that there is no global justification for the principle of simplicity in general. Instead, its legitimacy depends on researchers' substantive background assumptions about the way the world is in specific research contexts. Hence, what makes the principle of simplicity reasonable in one research context may be different from that in another. If proponents of different hypotheses have different background assumptions about the phenomenon under investigation, appeals to simplicity alone may not be able to justify privileging more parsimonious hypotheses. In the case of checkerboard distributions, proponents of the interspecific competition hypothesis tend to think that in a real biological context, it is very unlikely that the colonization of islands by birds is a purely random process. By contrast, proponents of null-model-based hypothesis testing think that it is problematic to exclude the random colonization hypothesis from the very beginning without testing it, which is why they urge researchers to conduct null-model-based hypothesis testing. However, if one chooses to privilege the random colonization hypothesis by appealing to simplicity, she needs to explain why the simpler hypothesis is more likely to be the true explanation of the phenomenon in this particular context.

As a brief summary, my analysis in this section reveals another important disanalogy between traditional statistical hypothesis testing and null-model-based hypothesis testing. For traditional statistical hypothesis testing used in well-controlled experimental research, since the proper control of variables is in place, if there is no statistically significant difference between the control and treatment groups with respect

to the statistics of interest, one is justified to maintain the null hypothesis and reject the alternative hypothesis. In null-model-based hypothesis testing, however, because of the equifinality of thermodynamically open systems and the lack of proper control of variables, one is not justified to reject the alternative hypothesis even when the simulated data match the empirical data.

3.2.3 The issue with the size of datasets

In null-model-based hypothesis testing, phrases such as "comparing simulated data with empirical data" are rhetorically powerful and epistemically appealing because they leave people with the impression that the comparison involved here is analogous to the comparison between data from the control and treatment groups in an experimental setting. However, while a comparison procedure does exist in null-model-based hypothesis testing, the datasets that are compared may not be a good analog to those in traditional statistical hypothesis testing.

To test a cause-and-effect relationship between two variables, the size of both the control and treatment groups should be large enough in order to guarantee the statistical power of the test. The specific minimum requirement is based on the evaluation of the context of each specific test. In any case, if the sample size is too small, one is not justified to make any causal inference based on the test. For example, if there are thirty subjects in the control group and only one subject in the treatment group, one is not justified to reject the alternative hypothesis even if there is no statistically significant difference between the results of the two groups, because the statistical power of such a test is so weak.

In null-model-based hypothesis testing, sample size is not inherently a problem for the simulated dataset because one can conduct the randomization simulation multiple times, and each round of simulation will contribute a data point for the statistic of interest. In the case of species co-occurrence studies, for example, each random matrix works as a simulated archipelago and contributes a data point about the number of non-coexisting species pairs. The minimal size of the simulated dataset can be guaranteed by examining multiple random matrices in the sample null space. But in the empirical dataset, there is actually only one data point for comparison in each test, which is the number of pairs of species that never co-exist in the actual archipelago. In other words, the comparison is conducted between a *null distribution*, which describes the probabilities of all the expected values of the number of non-coexisting pairs based on the simulated data generated by the null model, and a *single* empirical data point. While one can still test whether the value of the single empirical data point falls within the null distribution, it does not count as a proper analog to the comparison involved in traditional statistical hypothesis testing in experimental research.

3.3 Applying the analysis results

I have provided three reasons to show that null-model-based hypothesis testing is not an appropriate approximation of traditional statistical hypothesis testing in experimental research. Maybe this is an obvious point, but it does not always get enough attention in the discussion of null-hypothesis testing in the biological sciences, even among philosophers who aim to critically evaluate its use in specific cases. In this section, I will

apply the results of my critical analysis to a particular philosophical discussion of null hypotheses and null models.

In a recent paper, Bausman and Halina (2018) evaluate the use of what they call the "pseudo-null strategy" in explaining relative species abundance (hereafter RSA) distributions, i.e., the relative commonness or rarity of different species on the same trophic level of an ecological community. The traditional way to explain RSA patterns is to appeal to niche differences. Every species has acquired a unique set of traits that allow it to be adapted to a particular environment and occupy a unique niche. Different species can coexist in the same environment because they have different niches and make use of resources in different ways (Chase and Leibold, 2003). Hubbell (2001, 2006) has challenged this explanation by proposing a neutral theory of biodiversity. He assumes that all the individuals within a particular trophic level are ecologically similar regardless of their species identity, i.e., they have the same chance of reproduction, death, immigration, and speciation. Hubbell uses this neutral assumption as a null hypothesis against which the niche-based hypothesis should be tested.

Bausman and Halina (2018) rightly point out that the neutral hypothesis is a pseudo-null hypothesis because compared with the hypothesis based on niche differences, it just appeals to a different set of processes, which include reproduction, death, immigration, and speciation, to explain RSA distributions. What is more relevant to this chapter is their suggestion about what counts as a genuine null hypothesis in this case:

> Community ecologists have sampled communities from all over the world and used the observed distributions to test whether *ecological selection* is operating. The appropriate statistical null hypothesis for such tests is that the observed species distributions will not differ significantly from what we would expect if individuals of different species were *distributed at*

> *random* in space and time […]. (Bausman and Halina, 2018, p. 11, my italics)

Their suggestion is actually very similar to Connor and Simberloff's (1979) strategy, i.e., building a model in which individuals of different species are randomly distributed and then comparing the simulated data generated by this model with the empirical data collected from actual ecological communities. And the random distribution hypothesis is regarded as the null hypothesis. Not surprisingly, then, it suffers from the same problems as Connor and Simberloff's strategy. First, the authors' claim about the appropriate null hypothesis could be potentially misleading because they do not explicitly point out what the alternative hypothesis is given the statistical null hypothesis they suggest. If the alternative hypothesis is that the observed species distributions are the result of ecological selection, then it suffers from the same problem as the case of species co-occurrence studies, because the random distribution hypothesis that the authors suggest (the supposed null hypothesis) and the ecological selection hypothesis (the supposed alternative hypothesis) are not collectively exhaustive. This example reminds us again that whether a hypothesis counts as an appropriate null hypothesis is not solely determined by its own content, but is also influenced by the choice of its alternative hypothesis. One cannot take for granted that a hypothesis is an appropriate statistical null so long as it claims that a phenomenon is the result of some random processes or can be expected by chance alone.

Bausman and Halina may reply to this critique by claiming that the corresponding alternative hypothesis is not the ecological selection hypothesis, but the hypothesis that RSA distributions are *not* the result of random distribution. But this change does not

solve the problem of lacking proper control of variables. RSA distributions can be influenced by many processes, such as selection due to niche differences, ecological drift (random birth and death), immigration, and speciation. It is possible that the same distribution pattern of RSA can be produced through different combinations of those processes. So even if the simulated data match the empirical data, one is not justified to reject the alternative hypothesis and maintain the null.

The issue of dataset size also exists. In RSA studies, the unit of analysis is not the value of the point estimation of a statistic, but a *distribution pattern*. Through the random distribution model, one may be able to collect a set of distribution patterns by conducting the random simulation multiple times. But in the actual ecological community, one can only obtain a single distribution pattern of RSA for each trophic level. So what is compared is a set of distribution patterns from the simulated data and a single distribution pattern from the empirical data. This comparison fails to be a proper approximation to the comparison conducted in traditional statistical hypothesis testing in experimental research.

4. The possible use and limitations of null-model-based hypothesis testing

In the last section, I argued that null-model-based hypothesis testing cannot be justified as an appropriate analog to traditional statistical hypothesis testing in well-designed experimental research. But this does not mean that null-model-based hypothesis testing cannot be of any use at all. To better demonstrate the possible use of this strategy, I will make a comparison between Connor and Simberloff's (1979) null model of species co-occurrences and Schelling's (1978) model of segregation. I will argue that although these two kinds of models are constructed in very different ways, both of them can work as a

way to challenge our commonsense judgments about what could have produced a seemingly unusual pattern.

4.1 Challenging "common sense" by providing how-possibly explanations

In his book *Micromotives and Macrobehavior*, Schelling (1978) presents a very simple model to study the segregation of people in neighborhoods. His model is based on a grid representing a community. Suppose that residents in this community belong to two different groups, and the distinction between the groups can be made based on any reasonable criterion, such as people's racial identity, language, religion, or occupation. Each square in the grid can be either empty or occupied by a resident, and each resident has a minimum requirement of their neighborhood, such as that at least one-third of immediate neighbors be of the same group as the resident. The simulation starts from a random distribution of two groups on the grid. Each individual takes turns to decide whether they are content with their neighborhood. For those who are not, as a rule they will move to the closest empty square that satisfies their requirement. It turns out that the initial integrated distribution of two groups becomes strongly segregated when all the residents are content with their neighborhood after a number of rounds. And the outcome is robust when one alters the overall ratio of two groups, residents' minimum requirement of their neighborhood, the initial distribution, etc.

So what is the relevance of Schelling's model of segregation to our evaluation of the possible use of null models? After all, they are constructed in very different ways. The answer is that both Connor and Simberloff's null model of species co-occurrences and Schelling's model of segregation can be interpreted as a way to challenge the

commonly held explanation of a seemingly unusual pattern by providing an alternative how-possibly explanation.

As I mentioned earlier, Schelling's model can be used to study the segregation of any two different groups in a community. Suppose that we specify the two groups in his model as two racial groups (such as black and white people), then this model can be used to study racial residential segregation in neighborhoods. More specifically, Schelling's model can be used to show that patterns of racial residential segregation can result from individual choices based on small preferences for similarity that are not racist in the sense of being entirely intolerant of racial diversity. This challenges the commonly held view that racial residential segregation is due to the presence of extreme racist attitudes. By using the word "challenge," I do not mean that Schelling's model refutes or falsifies the categorical racism explanation; likewise, I do not claim that his model describes how racial residential segregation *actually* forms. Nor does it follow that racist problems do not exist or are not severe. Rather, it just provides another possible explanation. If both explanations are compatible with the emergence of segregation patterns, then *without further evidence* one cannot take for granted that the observation of racial residential segregation implies categorical intolerance of racial diversity.

Similarly, in the case of species co-occurrence studies, if the simulated data generated by Connor and Simberloff's null model are consistent with the empirical data collected from the actual archipelago with respect to the statistic of interest, then their model shows that the existence of checkerboard distributions might just be the result of random colonization. This alternative explanation challenges the prevailing view that checkerboard distribution patterns result from interspecific competition. Again, it does

not follow that checkerboard distributions are *indeed* the result of random colonization, or that relevant species do not compete in reality. Nevertheless, it shows that *without further evidence* one cannot take for granted that exclusive competition among bird species actually happens and causes checkerboard distributions.

A possible objection to my analysis is that since in this chapter I do not aim to deal with the technical controversies over how to build an appropriate null model, if it turns out that those issues cannot be solved, then the possible use that I propose for this strategy would not be available. I agree. Whether the strategy of null-model-based hypothesis testing can *actually* be useful does rely on whether an appropriate null model can be constructed. This is why I employ the term "possible use" throughout this chapter. Nevertheless, my analysis can still contribute to the discussion by showing the *scope* of the use of this strategy, i.e., what it might be able to do and what it absolutely cannot do. As I have shown, even if it is possible to construct a truly null model, null-model-based hypothesis testing still fails to be an appropriate analog of traditional statistical hypothesis testing, given the reasons provided in Section 3. Instead, its possible use resides in its role of providing a way to challenge scientists' commonsense judgments about how a seemingly unusual pattern could have come to be.

4.2 The limitations of null-model-based hypothesis testing

Despite the possible use, null-model-based hypothesis testing still carries severe limitations. In Section 3, I showed that null-model-based hypothesis testing cannot test whether a particular process or mechanism such as interspecific competition is responsible for the formation of certain patterns. Connor and Simberloff (1983, p. 464)

explicitly acknowledge this limitation by noting that "[w]ithout further evidence, probably of an experimental nature, one can neither eliminate any particular causal mechanism, nor conclude that a particular mechanism has operated."

Another limitation of this strategy is that the null model lacks the potential for dealing with other problems via further refinements and modifications. The null model is constructed to test the hypothesis that the existence of a pattern is the result of random processes or can be expected by chance alone. No matter whether this hypothesis can be rejected, once the test is conducted, the null model's mission is done. It may be argued that the null model can be further revised or made more complex for other uses by changing its constraints. This method is possible in principle, but difficult to use in practice. The difficulty lies in how to construe the updated model when the constraints are changed, and it is usually unclear what the updated model is supposed to represent. It may also be argued that lacking the potential for dealing with other problems hardly amounts to a fatal issue. Since the null model is a bespoke model that is designed to test a particular hypothesis (i.e., the random process hypothesis), it does not matter so much if it cannot be further developed to deal with other problems. I agree that this is not a fatal problem for null-model-based hypothesis testing, but it is still a limitation; recognizing this limitation can help us understand why many biologists are not so interested in null-model-based hypothesis testing. Understood this way, my discussion of the null model's limitations is not so much a criticism as an observation.

5. Lessons from the debate

The controversy surrounding null-model-based hypothesis testing is commonly interpreted as a debate about the usefulness of null hypotheses and null models in the biological sciences, especially in ecology and biogeography. But it is also important to take notice of the deeper origin of this debate. The motivation behind Connor and Simberloff's advocacy of null-model-based hypothesis testing is their general dissatisfaction with the then prevailing "competitionist paradigm" in community ecology. According to some ecologists, "competition has been invoked as an explanation for patterns to such a degree that it is in danger of becoming a panchreston, a concept that can explain everything" (Rathcke, 1984, p. 383). In this extreme case, one might invent a competitionist explanation for almost any seemingly unusual pattern in ecological communities without sufficient evidence. Connor and Simberloff (1979, 1983) have repeatedly argued that the existence of checkerboard distributions per se is not evidence for one species being actively resisted by another, and that more compelling evidence, such as evidence based on detailed autecological study, field observation, or experimentation, should be provided to support the interspecific competition hypothesis.

Against this background, null-model-based hypothesis testing is used by its proponents as a way to challenge the "competitionists." If one can show that the empirical data is consistent with what would be expected by a null model, then merely identifying certain distribution patterns is not enough to support the commonly proposed competition hypothesis. Hence, ecologists like Connor and Simberloff are not really against the role of competition as a *possible* mechanism for producing certain patterns. What concerns them is the lack of compelling evidence for many competitionist

explanations of ecological patterns. As Simberloff emphasized, “I’ve never said that there is no competition, that competition isn’t important in generating patterns in nature […]. All I’ve been addressing is the canons of evidence” (Simberloff as quoted in Lewin, 1983, p. 639).

But this is not the only thing that they want to contend. Connor and Simberloff (1979) were deeply inspired by Karl Popper’s falsificationism and thought that science progresses by proposing testable hypotheses and then trying to falsify them. Hence, besides requiring more compelling evidence, they also argued that proponents of the competition hypothesis (or any non-random hypothesis) should first try to falsify or reject a null hypothesis stating that the patterns under investigation are generated by random processes. It is this requirement that stirred up the controversy because it is intended to work as a *normative* claim about how research *should* be conducted, which puts extra epistemic responsibility on the side of competitionists.

We should be careful about the relationship between Connor and Simberloff’s concern about evidence and their normative claim about using null-model-based hypothesis testing. First, while null-model-based hypothesis testing might be useful by working as a way to challenge competitionist hypotheses of ecological patterns, its usefulness is not a necessary condition in order to criticize the “competitionist paradigm” with respect to the lack of compelling evidence. In other words, even if it turns out that the technical problems of constructing an appropriate null model cannot be solved, and null-model-based hypothesis testing is not useful at all, Connor and Simberloff’s call for more compelling evidence will remain valid. Second, if Connor and Simberloff’s primary concern is about the evidence for competitionist explanations, then null-model-based

hypothesis testing is neither a sufficient nor a necessary way for competitionists to deal with this critique. It is not necessary because competitionists can reply to their critics by collecting more compelling evidence through detailed autecological study, field observation, or experimentation without having to conduct a null-hypothesis test. It is not sufficient because even if competitionists successfully reject the null hypothesis, they might still lack the kind of evidence for their competitionist hypothesis demanded by their critics. Hence, competitionists do not have the responsibility to first conduct null-model-based hypothesis testing before pursuing their own hypotheses.

In sum, by focusing their attention excessively on null hypotheses and null models, both sides, including Connor and Simberloff themselves, deviate from the initial problem of the lack of direct evidence. Although Connor and Simberloff are absolutely right in claiming that more direct evidence is needed in order to support the interspecific competition hypothesis, null-model-based hypothesis testing is not the way to obtain the kind of evidence that they demand.

6. Conclusion

Null-model-based hypothesis testing has been used in many fields of biology, but its usefulness remains a concern. Although proponents of this method usually think that it is analogous to traditional statistical null-hypothesis testing in experimental research, I have shown that this analogy is not justified. Also, the random process hypothesis should not be privileged as a null hypothesis that biologists must try to reject before pursuing other hypotheses. But this does not mean that null-model-based hypothesis testing is necessarily useless. When trying to explain patterns in nature, biologists usually assume

that they are produced by specific causal factors, while ignoring the possibility that those seemingly unusual patterns are the result of random processes. By explicitly testing the random process hypothesis, null-model-based hypothesis testing might work as a way to challenge scientists' commonsense judgments about what count as unusual patterns and how those patterns could have come to be. Despite this possible use, researchers should also pay attention to the limitation of null-model-based hypothesis testing: the null model cannot be used to test whether a particular process or mechanism is responsible for the formation of certain patterns; it lacks the potential for dealing with other problems via further development; it cannot provide direct evidence for any non-random hypothesis.

Chapter 3: In what sense can neutral theory work as a baseline model?

1. Introduction

One of the most debated theories in modern ecology is the neutral theory of biodiversity (Hubbell, 2001). It claims that many biodiversity patterns in ecological communities can be explained by assuming that individuals of different species at the same trophic level are ecologically equivalent. Such a theory stands in stark contrast with the traditional approach to understanding community assembly, which explicitly invokes niche differences among species to explain biodiversity patterns in ecological communities (MacArthur, 1957; Chase and Leibold, 2003).

Given its radical assumption, it is not surprising that neutral theory of biodiversity has incurred strong criticisms since its proposal. As a response, supporters of neutral theory have appealed to several different strategies to defend its use. One of these strategies states that similar to the ideal gas model in physics, neutral models in ecology can be regarded as baseline models, which serve as a simple starting point for further research. When a neutral model fails, more complex non-neutral models can be constructed by adding more complexity into the neutral model.

This chapter aims to give a critical examination of the claim that neutral models in ecology can be regarded as baseline models. I will argue that whether a model counts as a baseline model depends on what type of phenomena it is intended to address and which models it is compared with. In the debate between neutral theory and niche-based theory, a neutral model should not be regarded as a baseline model relative to classical niche-

based models from a process-based perspective. As an implication, neutral models do not have methodological priority over niche-based models.

2. Two approaches to explaining biodiversity patterns in ecological communities

Community ecology is the study of patterns in the diversity, abundance, and composition of species in ecological communities as well as the processes underlying those patterns. One of the patterns of special interest to community ecologists is the distribution of relative species abundance (hereafter RSA), which describes the relative commonness or rarity of different species within the same ecological community.

The traditional way to explain RSA patterns is to appeal to niche differences. Every species has acquired a unique set of traits that allow it to be adapted to a particular environment and occupy a unique niche. Different species can coexist in the same environment because they have different niches and make use of resources in more or less different ways. Hence, RSA patterns can be explained by considering the partitioning of niches among different species. There are a variety of niche-based models of RSA, of which a classical one is MacArthur's (1957) broken-stick model. According to this model, the environment of an ecological community is compared to a stick with certain length. Suppose that there are n species in this community. In order to measure the relative abundance of these n species, $n - 1$ points are thrown onto the stick and break it into n segments. The length of a segment is proportional to the abundance of the species corresponding to that segment. Although the stick is used by MacArthur to refer to the environment in general, it can be further specified in different cases. For example, it can stand for an important resource competed for by different species. Also, the stick can be

broken in different ways. The method introduced above assumes that species in this community occupy non-overlapping, continuous niches.

Neutral theory, however, takes a very different approach. Instead of considering niche partitioning among different species, it adopts a stochastic dynamical approach to explaining biodiversity patterns in ecological communities. There exist different versions of neutral theory in the ecology literature. For the sake of discussion, here I only introduce the most influential version of them, that is, Hubbell's (2001) unified neutral theory of biodiversity.

There are two important assumptions in Hubbell's neutral theory. One is the neutrality (or ecological equivalence) assumption: All the individuals within a particular trophic level in an ecological community have the same probability of birth, death, and dispersal on a per capita basis, regardless of their species identity. In other words, this theory ignores the niche differences among different species in an ecological community. This is also why it is called "neutral theory." Notice that the neutrality assumption does not imply that there are no interactions, such as competition, among individuals. Instead, it allows interactions among individuals of different species as long as those interactions are symmetrical. Since resources available in a given community are limited, there should be competitions among individuals. But according to the neutrality assumption, individuals of different species are equal competitors.

The other is the zero-sum assumption. According to this assumption, ecological communities are always saturated, and community size – the total number of individuals in an ecological community – is held constant. In such a community, no species can increase in abundance without a matching decrease in the collective abundance of all the

other species. In other words, the dynamics of ecological communities are essentially a zero-sum game.

When an individual in a local community dies, its empty space will be refilled by another. This new individual can be reproduced by the same or a different species within the local community; it can also migrate from the metacommunity. By including random birth, death, migration, and speciation into a stochastic dynamical model, neutral theory is intended to predict or explain various biodiversity patterns in ecological communities at equilibrium, especially patterns of RSA.

3. The interpretation of neutral models as baseline models

Hubbell's neutral theory of biodiversity has elicited strong criticism since its proposal, which is no surprise given its radical and obviously false neutrality assumption. As McGill, Maurer, and Weiser (2006, p. 1411) vividly summarize, "This contradicts 100 years of community ecology." As a response, advocates of neutral theory have developed several different strategies to justify its use in ecology. One strategy, which is the focus of this chapter, is to argue that neutral models can work as "baseline models":

> "[N]eutral theory has a dual instrumentalist function: like any other theory, it can be used to predict patterns, but unlike many other theories, it is well positioned to act as a starting point, a baseline model to which one can later add more ecological mechanisms. It is exactly when it makes predictions that are not supported by empirical data that this second role is played." (Wennekes, Rosindell, and Etienne, 2012, p. 265)

Although there are quite a few cases where neutral models make very accurate predictions of diversity patterns in ecological communities (Hubbell, 2001), failing cases are also accumulating (Dornelas, Connolly, and Hughes, 2006; McGill, Maurer, and

Weiser, 2006). The second role described in the above quote, i.e., the role of acting as a baseline model, provides a methodological justification for neutral theory, and a crucial implication of this justification is that the usefulness of neutral theory would not be undermined by its inability to match some empirical data. When a particular neutral model fails to make accurate predictions, the ecologist can simply complicate the model by including more factors, such as niche differences, to provide a better fit to empirical data. This justification is intuitively appealing – there seems to be nothing wrong with starting from a simple model and adding more complexity when needed. Hence, it won't hurt if the ecologist starts with a neutral model.

Advocates of neutral theory are not merely arguing that neutral models *can* be used in ecology; in several other places, they also seem to think that neutral models have methodological priority over niche-based models:

> "[W]e argue that neutral theory should […] (be seen) as a baseline model that contains necessary ingredients that more advanced models should often also contain (…). We believe that starting from neutral theory is much easier than starting from a model that assumes niche differentiation from the outset. There might be other simple starting points as well." (Wennekes, Rosindell, and Etienne, 2012, p. 265)

As I mentioned earlier, there have been quite a few cases where neutral models make very accurate predictions of ecological patterns. These successes make advocates of neutral theory believe that niche differences, although having long attracted biologists' attention, are not always necessary for predicting and explaining biodiversity patterns in ecological communities. This judgment provides a ground for the belief that there exists a methodological asymmetry between a neutral model and a niche-based model. Since a neutral model is thought to contain essential factors that other models should also include,

when its predication fails to match the empirical data, one can learn something about what missing biological factors are needed to improve it. But it is more difficult to draw such conclusions from niche-based models, because failure could result from inclusion of incorrect details.

Advocates of neutral theory also justify the role of neutral models as baseline models by linking them with the ideal gas model in physics: "Ideal gases do not exist, neither do neutral communities. Similar to the kinetic theory of ideal gases in physics, neutral theory is a basic theory that provides the essential ingredients to further explore theories that involve more complex assumptions" (Alonso, Etienne, and McKane, 2006, 451).

Although the argument that neutral models are baseline models does not have to rely on the analogy between ecological neutral models and the ideal gas model, the seeming similarity between these two kinds of models does help add extra rhetorical power to the argument. The basic idea is that if the ideal gas model can be regarded as a baseline model in physics, then, by the same token, a neutral model can also be regarded as a baseline model in ecology. Since the usefulness of the ideal gas model has been widely accepted in physics, there should be similar reasons to accept the usefulness of neutral models in ecology.

4. Evaluating neutral models' status as baseline models

In the last section, I introduced a strategy that has been employed to justify the use of neutral theory in ecology: a neutral model can be thought of as a baseline model. In this section, I will give a more formal characterization of baseline model. Given this

characterization, I will then examine whether and, if so, in what sense both the ideal gas model and a neutral model can work as a baseline model.

4.1 What is a baseline model?

Although the term "baseline model" appears quite frequently in the scientific literature, it does not catch much attention from philosophers of science (for an exception, see Bausman, 2018). In general, it is a term that has been loosely used in the scientific literature without being clearly defined. In order to better evaluate a model's status as a baseline model in science, I give a more formal characterization of baseline model as follows:

> Model A is a baseline model relative to Model B if and only if A contains necessary factors that must also be considered in B in order to address certain type(s) of phenomena in a domain, and B can be constructed by adding more complexity into A.

According to this characterization, whether a model counts as a baseline model depends on what type of phenomena it is intended to address and which models it is compared with. It may be the case that a model works as a baseline model relative to one model, but not relative to another.

Labeling a model as a baseline model has several important implications. First, it assumes that the factors included in this model are causally relevant and non-negligible for addressing certain type(s) of phenomena in a domain. Hence, accepting a model as a baseline model means that the other models based on this model should also include the factors represented in the baseline model. This is a non-trivial empirical assumption,

given that one of the most challenging tasks in scientific modelling is to figure out which factors are causally relevant and which are not.

Second, labeling a model as a baseline model confers it a kind of methodological priority over those models that it is compared with. Since a baseline model is used as a starting point, if it can provide an accurate predication or an adequate explanation of the phenomenon under investigation, then there is no need to construct more complicated models. Besides, even when more complicated models do need to be constructed, the way they are constructed will still be constrained by the structure of the baseline model.

4.2 The ideal gas model as a baseline model

As I mentioned in Section 3, advocates of neutral theory have tried to establish an analogy between neutral models and the ideal gas model with respect to their status as baseline models. In this part, I will first examine the ideal gas model's status as a baseline model. I will show that according to the characterization of baseline model given above, the ideal gas model is indeed a baseline model relative to the other models in its relevant domain.

I start by giving a brief introduction of the ideal gas model. As its name indicates, an ideal gas is a kind of theoretical gas that does not exist in reality. There are several distinctive features of an ideal gas compared with real gases. First, in an ideal gas the volume of gas molecules is negligible compared with the space between them. Hence, gas molecules move around as points that do not occupy space. Second, there are no attractive or repulsive forces between gas molecules, which means that those molecules' movements are independent of each other unless collisions occur. Third, all the collisions,

no matter happening between gas molecules or between gas molecules and the wall of the container, are perfectly elastic. That is, there is no loss of kinetic energy of gas molecules in the collisions.

The behavior of an ideal gas obeys the ideal gas law: $PV = nRT$, where P is the gas pressure, V is the gas volume, n is the number of moles of gas molecules, R is a constant, and T is the temperature in Kelvin. What is especially interesting about the ideal gas model is that although an ideal gas does not exist in reality, the ideal gas model is thought of as being extremely useful in studies of the behavior of real gases. Its usefulness is mainly reflected in two aspects. On the one hand, some real gases do behave like an ideal gas in certain conditions. Generally speaking, a real gas behaves more like an ideal gas at higher temperature and lower pressure. On the other hand, even in cases where the ideal gas model fails to adequately describe the behavior of a real gas, more realistic models can be constructed by adding more complexity into the ideal gas model. For example, in order to provide a better description of the behavior of real gases, van der Waals (1873) constructed a more realistic model by taking into account molecular volume and intermolecular forces. The mathematical formulation of this model, which is known as the van der Waals equation, is as follows:

$$\left(P + \frac{an^2}{V^2}\right)(V - nb) = nRT$$

where a is a parameter associated with intermolecular attraction, and b is a parameter associated with the volume of gas molecules. It is easy to notice the structural similarity between the van der Waals equation and the ideal gas law, because the former is obtained on the basis of the latter. More complicated models can be further constructed based on

the van der Waals equation. The genealogical relationship among these models is shown in Figure 3-1.

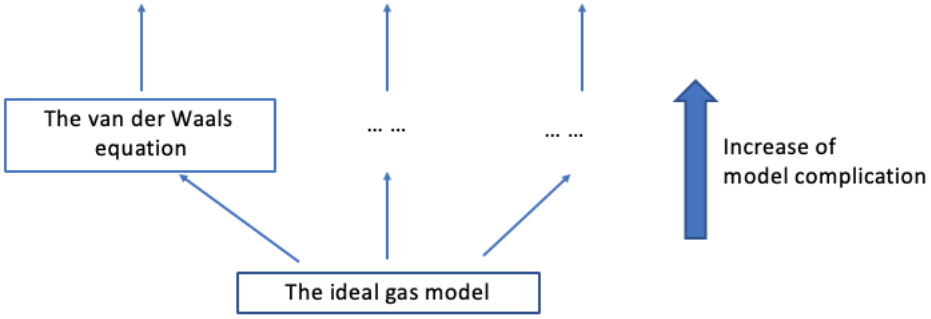


Figure 3-1. Genealogy of models used to describe the behavior of gases

Factors included in the ideal gas model, such as the collisions between gas molecules and the wall of the container, are essential factors that other gas models must also include. At the same time, the ideal gas model is also the simplest model that can be constructed in order to properly describe the behavior of real gases at least in some cases. Any further simplification will lead to the "breakdown" of the model: it would not be able to work in any case. Given this analysis, the ideal gas model is indeed a baseline model among the family of models that are designed to describe the behavior of real gases.

4.3 In what sense can a neutral model work as a baseline model?

In the last section, I showed that the ideal gas model is indeed a baseline model relative to a family of models in its relevant domain. In this section, I will consider the question of

whether a neutral model can work as a baseline model as the ideal gas model does. I start by introducing Mark Vellend's general theory of community ecology and then use it as a framework to examine neutral models' status as baseline models.

Community ecology is considered by some ecologists as "a mess" (Lawton, 1999), which consists of numerous theories and models but lacks an overarching conceptual framework to organize them. Vellend proposes a general theory of community ecology with the aim of achieving some kind of conceptual synthesis in this field from a process perspective, which first appeared in a review paper (Vellend, 2010) and was later developed into a whole book (Vellend, 2016). He argues that at the most general level, there are only four classes of process that can influence the dynamics and structure of ecological communities: selection, ecological drift, speciation, and dispersal. Selection refers to the deterministic interactions among species and between species and their environments that are related to the fitness differences among individuals of different species; ecological drift refers to stochastic processes such as random birth and death which lead to random changes in species' relative abundances; speciation is the formation of new species; dispersal is the movement of organisms across space. Vellend thinks that these four processes are analogous to the "big four" in population genetics: selection, genetic drift, mutation, and gene flow. Just as population genetics can be viewed as the study of the genetic composition of biological populations and its changes over time through the "big four" processes of evolution, community ecology can be seen as the study of patterns in ecological communities through the four general ecological processes.

Influenced by the controversy surrounding the ecological equivalence assumption in neutral theory, previous discussions have tended to characterize neutral models as

models excluding niche differences and focus on what is *missing* therein. Vellend's theory of community ecology provides a different perspective to look at neutral models. Instead of focusing on what is *missing* in a neutral model, the process-based framework encourages the ecologist to consider what processes are explicitly *included* in an ecological model. Under this framework, both niche-based models and neutral models are process-based models. The major difference between them is that they have focused on different ecological processes: A niche-based model is a model based on the process of selection, while a neutral model is a model that includes one or more processes of ecological drift, dispersal, and speciation.

I have mentioned about both "neutral theory" and "neutral model" in this chapter. Although there are different philosophical views of the relationship between theory and model, for the sake of discussion I will follow Rosindell et al. (2012, p. 203) and understand neutral theory as "an ensemble of different neutral models of community assembly." Given this, there is no such thing as *the* neutral model. Instead, what we have is a family of neutral models that share the ecological equivalence assumption. Vellend (2010, p. 183) surveys the literature and identifies four kinds of neutral models that correspond to four different combinations of the major processes in community ecology:

Neutral model I: drift
Neutral model II: drift and speciation
Neutral model III: drift and dispersal
Neutral model IV: drift, speciation, and dispersal

According to my characterization of baseline model in Section 4.1, whether a model counts as a baseline model depends on what types of phenomena it is intended to address and which models it is compared with. In the case of neutral models, the kinds of

phenomena under investigation are biodiversity patterns in ecological communities, such as patterns of relative species abundance. But neutral models are not the only kind of models that can be used to address community patterns. Other models include classical niche-based models and more complex non-neutral models. The genealogical relationship among these models is shown in Figure 3-2.

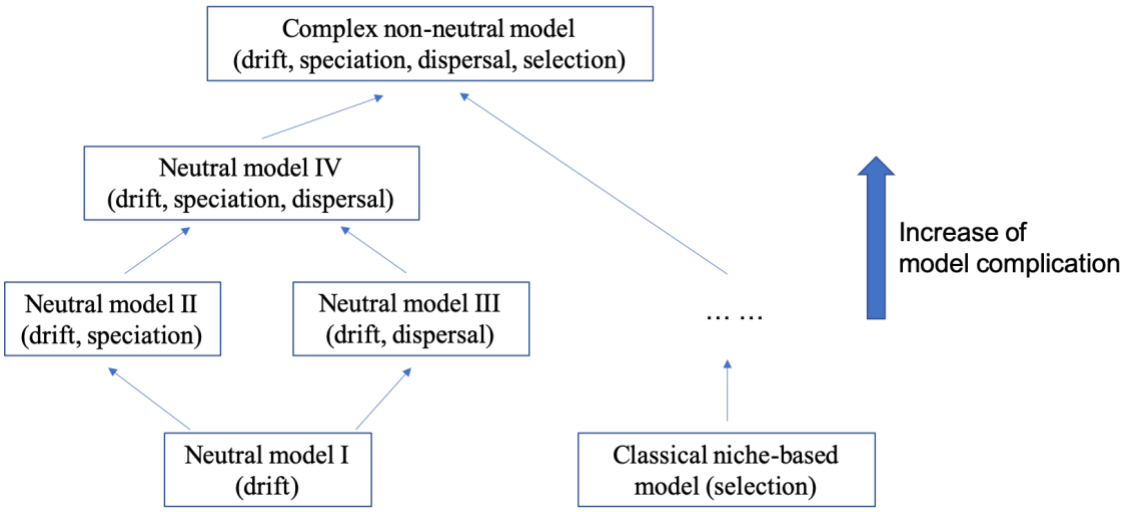


Figure 3-2. Genealogy of ecological models used to investigate biodiversity patterns in ecological communities (from a process-based perspective)

Let's first consider the relationship among the four neutral models. Neutral model I is a baseline model relative to all the other three neutral models, because the process contained in neutral model I (i.e., drift) is also included in the other neutral models. By contrast, II and III can be regarded as a baseline model relative to IV, but not relative to I, because both II and III contain some process that is not represented in I.

Perhaps a more interesting question is whether any of these neutral models can work as a baseline model relative to non-neutral models. Again, it depends on which non-

neutral models are under consideration. When compared with complex non-neutral models that include all the four general ecological processes (see the model at the top of Figure 3-2), all the four types of neutral models can be regarded as baseline models. This is because the processes contained in neutral models are also included in those more complex non-neutral models, which can be constructed by adding more processes into the neutral models. However, when compared with classical niche-based models that only include selection, none of the neutral models can be regarded as baseline models, because the processes contained in neutral models are not contained in classical niche-based models. In fact, there is no overlapping between neutral models and classical niche-based models with respect to the ecological processes that they contain. An important implication of this conclusion is that neutral models do not have methodological priority over classical niche-based models. They work as different starting points with different empirical assumptions about what factors are causally relevant for understanding the dynamics and structure of ecological communities.

4.4 The contrast between the ideal gas model and neutral models

If we compare the genealogy of ecological models in Figure 3-2 with the genealogy of gas models in Figure 3-1, we will find that they are different in one important aspect. In the family of gas models, all the models can trace back to a single starting point, i.e., the ideal gas model. In other words, the ideal gas model works as a baseline model for all the other models in the family. By contrast, in the family of ecological models, there are more than one single starting point. Hence, none of the models in the family, including neutral models, can work as a baseline model for all the other models.

What makes this difference? I suggest that this is due to the different nature of the phenomena to be addressed by these two families of models. The behavior of gas is influenced by many factors, such as the collision between gas molecules and the wall of the container, the volume of gas molecules, and intermolecular forces. Some of these factors, such as the volume of gas molecules and intermolecular forces, are negligible in modelling under certain circumstances, while some others, such as the collision between gas molecules and the wall of the container, are always important and must be considered in modeling under any circumstances. This is why it is possible to construct something like the ideal gas model which can serve as a baseline model for all the other models in its model family.

Biodiversity patterns in ecological communities are also the result of multiple causal factors. As I noted earlier, if we follow Vellend's process-based perspective, then community patterns can be understood as the outcome of one or more processes of selection, ecological drift, dispersal, and speciation. Vellend (2016, p. 175) has argued that "all high-level processes can be important determinants of community structure and dynamics," depending on the specific systems under investigation. But here I want to point out the other side of the coin: that is, none of these processes is always important in structuring ecological communities. Since the relative causal importance of different processes is very context-dependent, a process that plays an important role in one situation may be negligible in another. Hence, when trying to construct a model to explain or predict an ecological pattern, the ecologist does not have an overarching judgment about which processes are essential components of an explanation. Instead, which processes should be included in a model really depends on the type of

communities that one wants to investigate. This is also partly why modeling complex ecological communities can be very challenging.

5. Conclusion

In this chapter, I have examined the claim that neutral models in ecology can be regarded as baseline models. I have argued that whether a model counts as a baseline model depends on what type of phenomena it is intended to address and which models it is compared with. In a process-based perspective, neutral models are not baseline models relative to classical niche-based models. Hence, they should not have methodological priority over niche-based models. But this is not to deny the contribution and usefulness of neutral models in community ecology. On the one hand, neutral theory challenges the long-established view that niche differences are essential for explaining biodiversity patterns. On the other hand, it draws biologists' attention to processes such as ecological drift and dispersal whose importance in structuring ecological communities has long been underappreciated. Further research should focus on the conditions under which each of the major ecological processes plays important roles in determining the dynamics and structure of ecological communities.

Chapter 4: Empirical Adaptationism Revisited

1. Introduction

The debate about adaptationism has been one of the central topics within the philosophy of biology and evolutionary biology communities (Gould & Lewontin, 1979; Mayr, 1983; Godfrey-Smith, 1999, 2001; Lewens, 2009; Orzack & Forber, 2010). Instead of having a single, unified meaning, it refers to a family of views concerning the causal, methodological, or explanatory importance of natural selection in the course of evolution or in studies of evolutionary phenomena (Godfrey-Smith, 2001; Lewens, 2009; Orzack & Forber, 2010). One variety of these adaptationist views tries to make an empirical claim about the *causal power* of natural selection in evolution compared with non-selective evolutionary factors. Since this view is intended to make an empirical claim about nature, I will, for the sake of discussion, follow Godfrey-Smith (2001) and call it "empirical adaptationism."[8]

A number of philosophers and some biologists have tried to clarify the meaning of empirical adaptationism and define it in ways that do not make it trivially true or obviously false (e.g., Sober, 1987, 1998, 2000; Orzack & Sober, 1994; Godfrey-Smith, 2001; Lewens, 2009). Although these scholars may disagree on the details of how exactly empirical adaptationism should be formulated, they usually share, explicitly or implicitly, two assumptions about it: (1) Empirical adaptationism, while its truth is currently

[8] There are different ways to name or describe this kind of adaptationist view in the literature. For example, Sober (1998, p. 72) calls it "a non-trivial empirical thesis about the history of life"; Godfrey-Smith (2001) uses the term "empirical adaptationism"; Lewens (2009) further distinguishes between three forms of empirical adaptationism, and regards the view introduced here, which he calls "pan-selectionism," as merely one form of empirical adaptationism.

unknown or controversial, is an empirical claim about nature that is *scientifically testable* in the long run; (2) empirical adaptationism is *worth testing*.

In this chapter, I will reexamine these two assumptions and argue that both are mistaken given how empirical adaptationism is currently formulated. A series of conceptual and methodological difficulties makes testing empirical adaptationism in a biologically non-arbitrary way virtually impossible. Moreover, those who argue in favor of testing empirical adaptationism have yet to demonstrate the distinctive value as well as the necessity of conducing such a test. My analysis of the case of empirical adaptationism also provides reasons for scientists to reconsider the value and necessity of engaging in scientific debates involving the notion of overall relative causal importance.

2. The two themes of empirical adaptationism

I start by examining some influential formulations of empirical adaptationism in the literature. The purpose of doing so is not to assess which is the best formulation or to provide a new formulation based on existing ones. Rather, my aim is to figure out the *main themes* of empirical adaptationism in its various forms, i.e., what empirical adaptationism is about. Here are three influential formulations of empirical adaptationism given by different philosophers of biology:

> Natural selection has been the only important cause of most of the phenotypic traits found in most species. (Sober, 1998, p. 72)

> Natural selection is a powerful and ubiquitous force, and there are few constraints, except general and obvious ones, on the biological variation that fuels it. To a large degree, it is possible to predict and explain the outcome of evolutionary processes by attending only to the role played by selection. No other evolutionary factor has this degree of causal importance. (Godfrey-Smith, 2001, p. 336)

> [N]atural selection is the most significant of the evolutionary forces that act on populations. (Lewens, 2009, p. 162)

The above formulations of empirical adaptationism can be understood as different clusters of claims regarding at least one of the following two themes:

(a) The relationship between natural selection and various constraints on evolution
(b) The overall relative causal importance of natural selection in evolution compared with other evolutionary factors

These two themes are not necessarily bundled together; a biologist who makes an empirical claim about one theme may not necessarily take a position on the other. For example, while all three formulations above involve the overall relative causal importance of natural selection in evolution, only Godfrey-Smith's (2001) formulation contains an explicit claim regarding the relationship between natural selection and constraints. Although neither of the two themes alone is sufficient to capture the whole picture of empirical adaptationism, together they seem to provide a good coverage of the relevant debates. In the following sections, I will introduce these two themes in more detail and use them as a framework to examine the empirical testability of various claims under the label of empirical adaptationism.

3. The first theme: the relationship between natural selection and constraints on evolution

Although Darwin (1859, p. 6) explicitly acknowledged that natural selection is not the "exclusive means of modification," he is best known for his theory of evolution by *natural selection*. Here is a simplest case of how natural selection can drive the evolution of a trait in a given population: Heritable phenotypic variation arises among individuals

in a population. In a certain environment, different phenotypic variants may differ in their fitness, i.e., individuals carrying different types of phenotypes tend to have different rates of survival and reproduction. Over generations, natural selection will increase the frequency of the phenotype with the highest fitness and eventually drive it to fixation in the population.

This simple picture can be further complicated by taking into consideration various constraints. First, there may be *constraints on phenotypic variation*, which set limits on the raw material of natural selection. Among such constraints a much-discussed type is developmental constraint, which is typically defined as "a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system" (Maynard Smith et al., 1985, p. 266). For example, a phenotypic variant may be developmentally prohibited because the relevant mutation(s) lead to a lethal malformation in the process of embryological development. As a result, phenotypes that would have been favored by natural selection may not be able to appear in the population at all.

Other kinds of constraints do not limit the variety of phenotypes, but they may "get in the way" of natural selection by preventing the fittest phenotype from going to fixation in a population. These constraints may be properly called *constraints on the action of natural selection*. One example is the case of heterozygote superiority. Suppose that *A* and *a* are two alternative alleles at a locus in a diploid population, and the heterozygote *Aa* has a higher fitness than the two homozygotes *AA* and *aa*. Despite being favored by natural selection, the heterozygote *Aa* is not able to get fixed in the population because it cannot breed true: When two heterozygotes mate, there is always a probability

that some of their offspring are homozygotes. This fact imposes a genetic constraint on what natural selection can accomplish.

So what claims would an empirical adaptationist make regarding the relationship between natural selection and various constraints on evolution? One claim that has often been linked with empirical adaptationism is that natural selection is typically powerful enough to *overcome* or *conquer* various constraints (Amundson, 1994, p. 572; Stephens, 2007, p. 117). The constraints here can refer to either constraints on phenotypic variation or constraints on the action of natural selection, or both of them.

Let us first consider constraints on phenotypic variation. Amundson (1994, 572) describes a position called "hard adaptationism" as follows:

> All organic traits have adaptive values, and those adaptive values, via the principle of natural selection, provide the proper historical explanation of the existence of those traits. Any developmental constraints can be (and have been) overcome by the forces of natural selection.

What does it mean that a developmental constraint has been overcome? Consider a case where a phenotypic variant is developmentally prohibited. Sometimes new mutations arise and lead to the change of the developmental system such that the previously prohibited phenotypic variant is now allowed to be produced. In some sense, we can say that the developmental constraint has been overcome. But this change has nothing to do with the "power" of natural selection. Instead, it is due to the appearance of new mutations that alter the features of the developmental system. It may be argued that in order to really overcome a developmental constraint, the emerging new mutations must persist and spread in the population, which would have to be due to the operation of natural selection. Be that as it may, it is biologically inaccurate to claim that it is the

power of natural selection *per se* that overcomes the developmental constraint, and there is no reason to privilege the role of natural selection over mutation in this process.

The same conclusion applies to other kinds of constraints. Consider the much-discussed case of pleiotropy. Pleiotropy is the phenomenon that one gene has more than one phenotypic effect. Suppose that two phenotypes always co-occur among the individuals in a given population due to the effect of pleiotropy. If one phenotype has positive effects on its carrier's fitness while the other has negative effects, then the phenotype that could have been favored by natural selection for its positive effects may be eliminated from the population because of the stronger negative effects of the other phenotype. In this case, the beneficial phenotype fails to be selected not because it is prohibited to appear in the population, but because it is bundled together with another deleterious phenotype. As a response, Dawkins (1982, 35) has argued that "if a mutation has one beneficial effect and one harmful one, there is no reason why selection should not favour modifier genes that detach the two phenotypic effects, or that reduce the harmful effect while enhancing the beneficial one." This quote has often been used as an illustration of the view that natural selection is typically powerful enough to overcome pleiotropic constraints (Sober 1987, 115; Stephens 2007, 119).

Sober (1987, 116) comments that the detachment of two phenotypic effects in the case of pleiotropy is more indicative of the power of mutation rather than the power of natural selection. Although I am sympathetic to Sober's comment, I take it to be problematic to interpret Dawkins as saying that the power of natural selection per se can break the pleiotropic link between phenotypic effects. In fact, what Dawkins (1982, 35) wants to argue is that pleiotropy is not a static and unchangeable property of certain

genes, and he believes that it is possible to break the link between pleiotropic phenotypes when certain modifier genes emerge in a population and get selected. Hence, he would presumably agree that the detachment of pleiotropic phenotypes, when happens, is not merely due to the power of natural selection.

An alternative way to depict the relationship between natural selection and constraints is to claim that there are few constraints on the raw material of natural selection without explicitly attributing this rareness of constraints to the power of natural selection. For example, Godfrey-Smith's formulation of empirical adaptationism includes the claim that "there are few constraints, except general and obvious ones, on the biological variation that fuels it [natural selection]" (Godfrey-Smith, 2001, p. 336). An empirical adaptationist holding this view may concede that natural selection per se cannot overcome constraints, but nevertheless emphasizes the rareness of constraints on phenotypic variation in the actual biological world.

However, this formulation of empirical adaptationism has its own problems. First, Godfrey-Smith's formulation excludes "general and obvious" constraints when emphasizing the rareness of constraints on phenotypic variation. But it is unclear what counts as a "general and obvious" constraint. In particular, whether a constraint is obvious or not can be a matter of subjectivity. A constraint that is obvious to one biologist may not be obvious to another with different expertise or background knowledge. Second, there is much vagueness about the quantifier "few." Claims with quantifiers like "few" may be testable in some cases. For example, if there is no constraint on phenotypic variation, then Godfrey-Smith's formulation of empirical adaptationism would be false. However, every biologist, including those holding various

forms of empirical adaptationism, agree that there *are* constraints on the range of phenotypic variation. So the question becomes: How many constraints count as few? Numerous specific examples can be found about such constraints, but it is unclear how many would be enough to refute the empirical adaptationist claim. Of course, one can stipulate that there are few constraints if and only if the number of constraints is smaller than a certain threshold value. While this would make the empirical adaptationist claim testable, it is testable only in a biologically arbitrary way.

The issues that I raise about the use of the quantifier "few" are not merely semantic nitpicking; they are real issues that must be addressed for anyone who decides to take the testability of empirical adaptationism seriously. Scientific debates concerning very general claims about nature, such as empirical adaptationism, usually involve using quantifiers, but the impact of such use on the testability of general claims has not garnered much philosophical attention (but see Beatty (1997) for an exception). If biologists cannot achieve some consensus on what counts as "few constraints" in a biologically meaningful way, then it is very unlikely that debates about empirical adaptationism can be resolved by merely accumulating more empirical studies.

One possible way to clarify the meaning of "few" is to compare the number of prohibited phenotypic variants due to the existence of constraints and the number of variants actually appearing in a population. This approach relies not on the specific number of constraints, but on their causal effects on phenotypic variety. Fig. 4-1 is a typical way to illustrate the influence of constraints on the range of discrete phenotypic variants available for selection (Sober, 1998, p. 79). $\{P_1, P_2, \ldots, P_n, \ldots, P_{n+m}\}$ refers to the set of conceivable phenotypic variants in the absence of constraints; $\{P_1, P_2, \ldots, P_n\}$ is the

set of phenotypic variants that actually appear in the population; P_1 is the variant that becomes fixed in the population due to the action of natural selection. Given this setting, *m* of the *n*+*m* phenotypic variants are prohibited from appearing due to the existence of constraints. To clarify the meaning of "few," it may be stipulated that there are few constraints on the phenotypic variation of a trait if and only if the number of phenotypic variants prohibited due to the existence of constraints (*m*) is smaller than the number of variants actually appearing in the population (*n*).

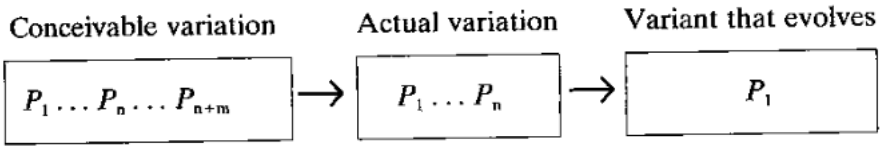


Figure 4-1. The two-stage process of the evolution of a trait, from Sober (1998)

Although this definition seems to provide a more rigorous testing method, it still falls prey to the problem of terminological ambiguity, which in this case involves the concept of "conceivable variation." Sober (1998, 79) argues that it is impossible to be very precise about the value of *m* because the number of conceivable variants depends more on biologists' imaginations rather than on empirical facts. Hence, from a biologically perspective, it does not make much sense to compare the values of *m* and *n*.

I agree with Sober's conclusion, but for different reasons. First, the number of conceivable variants may be empirically determinable if the concept of "conceivable variation" is defined *relative to a particular constraint*. For example, conceivable variation can refer to the phenotypic variants that would be possible to appear in a

population if a particular constraint were absent. According to this definition, it is possible to estimate the number of conceivable variants by examining the actual variation in the population and studying the causal effects of a particular constraint. The problem, however, is that there is obviously more than one constraint for any group of evolving organisms. In one sense, the history of organic evolution is a history of cumulating constraints, which make the appearance of some traits less likely or even impossible and others more probable. The further we trace back the evolutionary history of a group of organisms, the more constraints we might be able to identify. When more and more constraints are loosened or removed, the number of conceivable variants would become larger and larger. Hence, the relative magnitudes of *m* and *n* depends on how far we would like to trace back the evolutionary history of a population and hence how many constraints are counterfactually removed.

In addition, the way Sober makes his argument reflects an inaccurate understanding of the role of constraints that is common in the literature. According to the illustration in Figure 4-1, $\{P_1, P_2, \ldots, P_n, \ldots, P_{n+m}\}$ shrinks to $\{P_1, P_2, \ldots, P_n\}$ due to the existence of various constraints. This typical way of depicting the effect of constraints seems to suggest that they can only play a "negative" role in evolution by prohibiting the production of certain conceivable phenotypic variants. However, if we switch our perspective, we may find that the so-called constraints can also play a "positive" role in evolution. Consider the case of developmental constraints. Developmental constraints are defined as biases on the production of variant phenotypes or limitations on phenotypic variability caused by the properties of the developmental system. But the properties that prohibit the production of certain phenotypic variants may also be the properties that

support the normal development of other variants. To use an analogy, the prohibitive role and the supportive role of certain properties of the developmental system are like the two sides of a coin: From one side we see developmental constraints, while from the other side we see support for new developmental opportunities. Here is an important implication of this more nuanced understanding of the nature of constraints: Biologically speaking, it is not very meaningful to ask the number of conceivable phenotypic variants in the absence of all constraints, since a developmental system without any constraints may not be able to produce any phenotypes at all.

In this section I examined two varieties of claims that empirical adaptationists might make about the relationship between natural selection and constraints on evolution. The first claim is that natural selection is typically powerful enough to overcome various constraints. I have shown that this claim is biologically inaccurate. The second claim is that there are few constraints on phenotypic variability. I have shown that the inherent vagueness of this claim makes it unamenable to empirical testing.

4. The second theme: the overall relative causal importance of natural selection in evolution

The second theme of empirical adaptationism concerns the *overall relative causal importance* of natural selection in evolution. A typical adaptationist claim regarding this theme is that natural selection is, in most cases, the most or the only important cause of phenotypic evolution. In order to test the truth of this claim, biologists need to proceed in two steps. First, they need to test whether natural selection is the most or the only important cause of the evolution of various *particular traits*. Second, they need to

calculate *how often* it is the case that natural selection is the most or the only important cause of the evolution of a trait.

Let's start with the first step. To be clear, the claim that natural selection is the *most* important cause of the evolution of a trait is different from the claim that natural selection is the *only* important cause of the evolution of a trait. The former claim does not deny the possibility of other evolutionary factors being causally important in the evolution of a trait, but simply emphasizes the causal superiority of natural selection over other evolutionary factors. The latter claim, however, regards the role of non-selective evolutionary factors as negligible in the evolution of a trait. Hence, there are actually two empirical adaptationist views regarding the second theme:

> (I) Natural selection is in most cases the *most* important cause of phenotypic evolution.
> (II) Natural selection is in most cases the *only* important cause of phenotypic evolution.

Notice that an empirical adaptationist who holds (I) may not accept the truth of (II). Hence, it is important to keep these two claims distinct. In the following, I will examine the testability of (I) and (II) respectively.

The testability of Claim (I)

Let us first consider claim (I): Natural selection is in most cases the *most* important cause of phenotypic evolution. The idea that natural selection is in some sense more important than other evolutionary factors has a long history in the development of evolutionary thinking. At the very end of the Introduction in the first edition of *On the Origin of Species*, Darwin claimed that "I am convinced that Natural Selection has been the *main*

but not exclusive means of modification" (Darwin, 1859, p. 6, my italics). In the fifth edition, he revised the wording and stated that "I am convinced that Natural Selection has been the *most important* but not the exclusive means of modification" (Darwin, 1869, p. 6, my italics). Darwin is not alone in this kind of thinking. For example, Jonathan Losos, a leading evolutionary biologist today, thinks that "evolution is the historical occurrence of change, and natural selection is one mechanism – *in most cases the most important* – that can cause it" (Losos, 2014, p. 3, my italics).

In the following, however, I will argue that it is not always possible to compare the relative causal importance of natural selection and other evolutionary factors. I will consider several cases where the evolution of a trait is influenced by both natural selection and a non-selective factor and show that in those cases it does not make sense to privilege one evolutionary factor as causally more important than the other.

Case 1: Suppose that a beneficial phenotypic variant that would have been favored by natural selection (labelled as T_1) fails to appear in a population because of the existence of a certain developmental constraint. As a result, natural selection favors an alternative phenotypic variant available in the population (labelled as T_2) and drives it to fixation, although T_2 would have a relatively lower fitness than T_1 if T_1 were allowed to develop. However, if the developmental constraint did not exist, the result would be entirely different. Natural selection would favor the initially prohibited variant T_1 and drive it to fixation. In this case, the developmental constraint and natural selection play different kinds of causal roles in the evolution of the focal trait. The developmental constraint determines which phenotypic variants are available in the population in the first place, while natural selection determines which of the available phenotypic variants

finally gets fixed in the population. It does not make sense to claim that one of these two evolutionary factors is a more important cause of evolution than the other.

Case 2: In his Shifting Balance Theory, Sewall Wright (1931, 1932) depicts a scenario where a large population is divided into many partially isolated subpopulations and its adaptive evolution is driven by the interaction between natural selection and genetic drift. The whole process can be understood as consisting of three phases (Skipper, 2002): In the first phase, genetic drift causes gene frequencies to fluctuate in subpopulations, allowing some of them to move across adaptive valleys and reach the base of a higher adaptive peak; in the second phase, natural selection operates within subpopulations, moving them to local adaptive peaks; in the third phase, organisms from more fit subpopulations migrate to less fit ones, and natural selection between subpopulations increases the average fitness of the whole large population.

It is clear that natural selection and genetic drift play different roles in the above scenario: Genetic drift helps subpopulations shift across adaptive valleys toward new, higher adaptive peaks; natural selection increases the average fitness of both each subpopulation and the whole population. However, it is unclear how we can compare the relative causal importance of natural selection and genetic drift. Without genetic drift, subpopulations will be held at the nearest adaptive peaks by natural selection, having little chance to move across the adaptive valleys toward a higher adaptive peak; without natural selection, cumulative adaptive changes are unlikely to occur, no matter in subpopulations or the whole population. In this situation, neither of these two evolutionary factors can be said to be causally more important than the other – both

natural selection and genetic drift play an essential role in the evolutionary process described above.

Case 3: Suppose that initially there exist three variants (V_1, V_2, V_3) of a trait in a population, and their fitness ranks as follows: Fitness (V_1) > Fitness (V_2) > Fitness (V_3). Among these three variants, V_1 and V_2 are new variants that have recently emerged in the population, each having a very low frequency. Suppose that V_1 is lost from the population due to the effect of random genetic drift. Among the remaining two variants, V_2 is favored by natural selection and spreads to fixation in the population. In this case, genetic drift eliminates the fittest variant from the population, while natural selection increases the frequency of the second fittest variant. Both genetic drift and natural selection are essential to explain why V_2 can eventually get fixed in the population, and there is no intelligible way to compare the relative causal importance between these two evolutionary factors.

I have analyzed three problematic cases where we are not allowed to compare the relative causal importance of natural selection and non-selective evolutionary factors in an intelligible way, and they are not intended to be exhaustive of all the problematic cases. The point is not that we cannot never make such comparison, but that it is not always possible to do so. Since testing claim (I) requires comparing the relative causal importance of natural selection and other evolutionary factors in individual cases, the existence of various problematic cases would seriously undermine the testability of the empirical adaptationist claim that "natural selection is in most cases the *most* important cause of phenotypic evolution."

Claim (II): Orzack and Sober's formulation of empirical adaptationism

I now turn to claim (II): Natural selection is in most cases the *only* important cause of phenotypic evolution. A formulation of empirical adaptationism like this has been proposed by Orzack and Sober.

Orzack and Sober (1994b) distinguish three propositions about the role of natural selection in the evolution of some individual trait *T* in a given population (p. 362):

> (U) Natural selection played some role in the evolution of *T*.
> (I) Natural selection was an important cause of the evolution of *T*.
> (O) Natural selection is a sufficient explanation of the evolution of *T*, and *T* is locally optimal.

Orzack and Sober think that proposition (O) best captures the adaptationist view on the evolution of a trait. Notice that proposition (O) per se is not a formulation of empirical adaptationism, because empirical adaptationism is not a claim about the role of natural selection in the evolution of a particular trait, but a general claim about the overall relative causal importance of natural selection in evolution. Given this, Orzack and Sober (1994b, p. 364) formulate the thesis of empirical adaptationism[9] as a generalized form of proposition (O):

> Natural selection is a sufficient explanation for most nonmolecular traits, and these traits are locally optimal.

How could biologists tell whether natural selection is a sufficient explanation of the evolution of a trait? Orzack and Sober suggest that this can be tested via an optimality model. An optimality model is a kind of "censored" model in which non-selective evolutionary processes such as genetic drift are ignored and only natural selection is described. Under this setting, the most adaptive variant of a trait among a set of

[9] Although Orzack and Sober (1994b) do not use the term "empirical adaptationism," it is clear that the kind of adaptationism discussed by them is intended to be an *empirical* claim about nature.

alternatives in a particular environment is expected to be selected and eventually driven to fixation in the population. If the optimality model's quantitative prediction about the optimal value of an individual trait in a given population fits the empirical data statistically, then natural selection would be a sufficient explanation of the evolution of that trait. Under these circumstances, natural selection is also said to be the *only* important cause of the evolution of the focal trait. Hence, in another place Sober (1998, p. 72) also formulates empirical adaptationism as follows:

> Natural selection has been the only important cause of most of the phenotypic traits found in most species.

For Orzack and Sober, claiming that natural selection is the only important cause of the evolution of a trait does not mean that it is the only cause at work. In these cases, non-selective evolutionary factors may still exist, but they play such a small role in the evolution of a trait that they can be ignored without loss of accuracy when predicting or explaining the evolutionary outcome of that trait. For example, since no biological population in reality is infinitely big, genetic drift always plays some role in the evolution of a population. But when the population is big enough, it is usually innocuous to ignore the effect of genetic drift when studying the evolution of a trait in that population.

It is worth emphasizing again that Orzack and Sober's formulation of empirical adaptationism is different from the claim (I) that natural selection is in most cases the *most* important cause of phenotypic evolution. One major benefit of formulating empirical adaptationism in Orzack and Sober's way is that it does not involve *directly comparing* the relative causal importance of natural selection and non-selective evolutionary factors, thus circumventing the comparison problem faced by the weaker

claim. This subtle but important difference has failed to be fully appreciated in the literature. For example, Resnik (1997, p. 42) describes Sober's definition of empirical adaptationism as the claim that "natural selection is the most important cause of most traits in most populations"; Lewens (2009, p. 163) summarizes Orzack and Sober's formulation of empirical adaptationism as the view that "selection is typically the most important evolutionary force." Both of them conflate Orzack and Sober's formulation of empirical adaptationism with claim (I).

Until now I have yet to analyze the testability of Orzack and Sober's version of empirical adaptationism. In the next section, I will discuss several methodological difficulties that may well undermine the testability of empirical adaptationism as envisaged by them.

5. Methodological difficulties in the long-run test of empirical adaptationism

Empirical adaptationism as formulated by Orzack and Sober is a *general* thesis about nature – a claim about the overall relative causal importance of natural selection in evolution. As an implication, the correctness of such a thesis cannot be assessed by testing the local optimality of a single phenotypic trait. Orzack and Sober are fully aware of the ensemble nature of such a test, and they suggest that empirical adaptationism is testable by accumulating the results of investigations of many traits:

> The test of adaptationism we advocate need not engender an interminable debate. Forty or 50 appropriately structured studies might well provide a reasonable assessment of adaptationism. For example, if 45 of the 50 tests lead to the conclusion that the trait in question is locally optimal, in our opinion one could conclude that adaptationism is correct. Attainment of some agreed-on number of tests should be a goal of evolutionary biologists. (In these days of the Human Genome Project, it may be appropriate – and perhaps even more useful – to organize a far cheaper Adaptationism Project in order to coordinate quantitative studies of

> optimality models.) […] [A] test of adaptationism of the size mentioned earlier might even be attainable in the next 10 yr or so. (Orzack & Sober, 1994b, pp. 377–378)

27 years have passed since Orzack and Sober made this proposal, but the kind of test envisaged by them has yet to be conducted. It is an interesting question why biologists, including Orzack himself, have not organized an Adaptationism Project to assess the correctness of empirical adaptationism. But even if biologists decided to implement such a project, they would have to first address a number of methodological difficulties to guarantee the validity of the test.

In an ideal case, biologists would have a complete list of all the phenotypic traits of all organisms in the history of life, and they are able to test in each case whether natural selection is sufficient to explain the evolution of a trait. Clearly, this is not a practical plan. A more feasible way to conduct the test is to choose a *representative* sample of all the phenotypic traits.

Several methodological issues need to be addressed in order to obtain such a representative sample. First, evolutionary biologists need to reach some kind of consensus on the number of traits to be studied in the sample. Orzack and Sober (1994b, p. 377) suggest that "[f]orty or 50 appropriately structured studies might well provide a reasonable assessment of adaptationism." But they provide no clue of how this number is determined and justified from a statistical point of view. Even if the issue of sample size can be resolved, another methodological difficulty remains, namely, how to select a sample of traits such that the testing result is representative of the overall relative causal importance of natural selection in the evolution of all the traits of all organisms appearing in the history of life.

It may be argued that statisticians have developed various sampling techniques to help ensure the representativeness of a sample. For example, if there are two colors of glass beads – red and blue – in a box and a researcher wants to know the proportion of the red ones, she can mix the beads sufficiently and select a sample of a certain size randomly. This sampling technique is called *simple random sampling*, and the underlying rationale is that in such a setting, every possible sample of the same size has the same probability of being selected during the process of sampling.

However, sampling methods like this may not be easily applied to the case of testing empirical adaptationism. One major goal of statistical research is to draw conclusions about the properties of populations via studying samples. By "population," or more precisely, "statistical population," I mean a group of individuals that a researcher wants to draw conclusions about, which can be either concrete objects such as glass beads, or abstract objects such as the possible moves of a chess player. From a statistical point of view, having a *well-defined* statistical population is essential for getting a representative sample of that population. A statistical population is well-defined if and only if there is a clear standard about what should be included in the population and each individual in the population is possible to be sampled during the time of investigation. In the case of glass beads, the statistical population is the collection of all the glass beads in the box, which is well-defined according to the preceding definition. Without the existence of this well-defined statistical population, it does not even make sense to ask whether a sample is representative, because the representativeness of a sample, by definition, is always relative to the statistical population that it is intended to provide information about.

Now consider the case of testing empirical adaptationism. What is the statistical population that biologists want to know about? A quick answer would be "all the traits of all organisms." But this answer is too vague to be helpful. For example, should structures like eyes or wings of different species be regarded as one trait? Or should each of them count as a different trait? A clue of answers to these questions may be found in the subtle changes in the way empirical adaptationism is formulated by Sober in different places:

> (i) Natural selection is a sufficient explanation for *most nonmolecular traits*, and these traits are locally optimal (Orzack and Sober, 1994b, p. 364, my italics).
>
> (ii) Natural selection has been the only important cause of *most of the phenotypic traits found in most species* (Sober, 1998, p. 72, my italics).
>
> (iii) *Most phenotypic traits in most populations* can be explained by a model in which selection is described and nonselective processes are ignored (Sober, 2000, p. 124, my italics).

Formulation (i) talks of nonmolecular traits (i.e., phenotypic traits)[10] in general. Formulation (ii) seems to suggest that analyses of phenotypic traits should be on the level of species. If so, structures such as eyes or wings of different species should each count as a different trait. Formulation (iii) goes one step further: Studies of the same trait in *different populations* of a species may yield different results. For example, a trait that is locally optimal in one population may not be so in another. Hence, it seems reasonable to regard studies of the same trait in different populations as different individual cases while sampling. Suppose that we adopt the granularity of analysis in formulation (iii), then the statistical population being studied would be all the phenotypic traits in each population of each species.

[10] Sober's discussion of empirical adaptationism focuses on nonmolecular traits.

However, such a statistical population is still poorly defined, which does not allow biologists to obtain a representative sample of it. Although the concept of trait is widely used in biology, it is notoriously difficult to define what a trait is. In a very general sense, a trait is simply a character state of an organism. But exactly what feature of an organism could be properly regarded as a trait depends on many factors, including facts of developmental processes of organisms (Wagner, 2001), the researcher's background theories and beliefs (Resnik, 1997), as well as the specific content of the research problem in question. Hence, different biologists would identify different collections of traits even within one population of one species, and the situation will be even worse when we consider all the populations of all species. But the problem goes beyond this.

In the case of glass beads, each glass bead in the box has the same probability of being selected in the process of sampling. In the case of testing empirical adaptationism, however, many features of organisms have no chance to be sampled because they have yet to be individuated by biologists as traits and hence cannot enter the sampling pool at all. In other words, the statistical population that is intended to include all the phenotypic traits in each population of each species is not well-defined, which makes it impossible to collect a representative sample thereof.

It may be argued that instead of trying to obtain a representative sample of all the possible phenotypic traits in each population of each species, biologists can just build a list of all the traits that have already been individuated and studied. If most of the already-studied traits are locally optimal, then the version of empirical adaptationism as formulated by Orzack and Sober is true. This approach does not really solve the problem

of representativeness. The way we distribute our scientific resources can influence our perception of the relative importance of natural selection in evolution (Beatty, 1987, pp. 53–54). The more scientific resources are distributed to studies on the apparent design of organisms and their relations of adaptedness to their environments, the more likely it is to find cases of local optimality. Similarly, the more funding is provided to studies on the role of non-selective evolutionary factors (such as genetic drift) in evolution, the more likely it is that counterexamples of optimality can be found. If the testing result of empirical adaptationism is simply a statistical summary of the results of biologists' previous studies, then this result would be more of a reflection of scientific resource distribution and biologists' research interest rather than what actually happens in nature. This observation poses a serious problem for those in favor of testing empirical adaptationism, for it contradicts with one of their core beliefs that empirical adaptationism is an empirical thesis about *nature*.

In this section, I have discussed a series of methodological difficulties of obtaining a representative sample in the test of empirical adaptationism. Although I use Orzack and Sober's proposal as a target of critique, my analysis reveals a general challenge for any serious attempt to test empirical adaptationism as a general thesis about nature. This challenge, in my view, makes testing empirical adaptationism in a biologically non-arbitrary way virtually impossible.

6. Rethinking the value and necessity of testing empirical adaptationism

The previous sections have focused on the testability of empirical adaptationism. I now turn to a different issue: Why should biologists care about the truth of this general thesis

at all? As mentioned earlier, a number of philosophers and some biologists have tried to clarify the meaning of empirical adaptationism and provide their own formulations. These scholars are not necessarily committed to the truth of empirical adaptationism. Instead, they regard as an empirical matter whether empirical adaptationism is true and leave the task of testing its truth to biologists. When doing so, they also assume that empirical adaptationism is worth testing. However, in the existing literature, there has been little explicit justification of why this should be the case.

In this section, I will consider four types of value that might be attached to the test of empirical adaptationism. It turns out that some of these values simply do not exist; the others either are trivial or can be achieved without having to test empirical adaptationism. Hence, none of them can be used to justify the necessity of conducting such a test. To be clear, the four types of value that I will consider below are not intended to be exhaustive of all conceivable values. Hence, my analysis in this section does not allow me to conclude that no other values of testing empirical adaptationism can be found in the future. Nevertheless, my argument, if succeeds, will show that those in favor of testing empirical adaptationism have yet to demonstrate the distinctive value as well as the necessity of conducting such a test.[11] Unless a proper justification can be provided, there seems no reason to assume that empirical adaptationism is worth testing.

[11] This argument should not overshadow the necessity of evaluating the testability of empirical adaptationism. Even if one can find some value in testing empirical adaptationism, the previous sections show that empirical adaptationism, as currently formulated, is not genuinely testable in practice.

6.1 Methodological heuristic value

As mentioned in the introduction, there are different kinds of adaptationism. Those in favor of testing empirical adaptationism may seek to argue for the necessity of such a test by appealing to the relationship between empirical adaptationism and another kind of adaptationist position – methodological adaptationism. Godfrey-Smith (2001, p. 337) defines methodological adaptationism as the following view: "The best way for scientists to approach biological systems is to look for features of adaptation and good design. Adaptation is a good 'organizing concept' for evolutionary research." Lloyd (2015), a representative critic of methodological adaptationism, formulates this research method in terms of the research question asked by its practitioners: A methodological adaptationist assumes, at the beginning of investigation, that a trait under consideration is an adaptation and asks "What is the function of this trait?"; given such a research question, they would try to look for adaptative explanations for the evolution of this trait.

Those in favor of testing empirical adaptationism may argue that many biologists are motivated to adopt methodological adaptationism in their actual scientific research because they believe the truth of empirical adaptationism: The belief in the power and ubiquity of natural selection in evolution motivates these researchers to assume, at the beginning of their investigation, that a trait is an adaptation until shown otherwise. For these researchers, it truly matters whether empirical adaptationism is correct or not, because methodological adaptationism – a widely-practiced methodology – is justified by the truth of empirical adaptationism. Given the central role of empirical adaptationism in motivating and justifying actual scientific practice, it is valuable and necessary to test this thesis.

This argument does not work because it fails to distinguish the *beliefs* that motivate someone to adopt a methodology and the *genuine justification* that is needed to defend such a methodology. It is perfectly possible that a methodological adaptationist is motivated to adopt this methodology because she *believes* that empirical adaptationism is true and that the truth of empirical adaptationism justifies the legitimacy of methodological adaptationism as a valid research strategy. However, the occurrence of such a situation does not mean that the justification of methodological adaptationism *actually* relies on the truth of empirical adaptationism. Godfrey-Smith (2001, p. 338) has shown that empirical adaptationism and methodological adaptationism are logically independent of each other. As a consequence, the truth or falsity of empirical adaptationism does not really bear on the justifiability of methodological adaptationism – even if empirical adaptationism turns out to be false, it does not exclude the possibility of methodological adaptationism being a valid and productive research strategy. Notice that I am not denying the fact that empirical adaptationist beliefs motivate some (or even many) biologists to adopt methodological adaptationism. But this fact does not guarantee the value and necessity of testing empirical adaptationism. To evaluate the validity of methodological adaptationism, we need to examine its merits (or problems) from a methodological perspective, rather than test the truth of empirical adaptationism.

This analysis is also supported by the actual critiques offered by opponents of methodological adaptationism. For example, in her systematic critique of methodological adaptationism, Lloyd (2015) objects to this research method by identifying various dangers that result from the logic of its research question, such as the lack of a stopping rule in pursuing adaptive explanations for the evolution of traits and the loss of ability to

evaluate and weigh evidence for alternative causal hypotheses. None of these critiques is based on the falsity of empirical adaptationism. Lloyd also proposes an alternative research strategy called the "evolutionary factors" framework, whose fundamental research question is "What evolutionary factors account for the form and distribution of this trait?". When discussing the relationship between this alternative framework and empirical adaptationism, she notes that "the evolutionary factors framework is independent of any commitment regarding empirical (or 'metaphysical') adaptationism" (p. 345). It goes beyond the scope of this chapter to evaluate whether the evolutionary factors framework is indeed a better alternative to methodological adaptationism. What is relevant here is that, for Lloyd, the reason why biologists should abandon methodological adaptationism and adopt the evolutionary factors framework has nothing to do with the truth or falsity of empirical adaptationism, but with the relative methodological superiority of the evolutionary factors framework in biological research.

6.2 Explanatory value

It may be argued that empirical adaptationism is worth testing because its truth (or falsity) has explanatory value. A piece of information has explanatory value in science if and only if it contributes to explaining certain scientific phenomena. Now the question is: Can we find any biological phenomenon whose explanation at least partly relies on the test result of empirical adaptationism? To the best of my knowledge, no such examples have ever been presented in the relevant literature. And in my view, the prospects for finding such examples are dim: Even if empirical adaptationism is testable, its truth (or falsity) is simply based on a statistical summary of the testing results of individual cases; it is

unclear how such a highly contingent and general fact can help to explain the occurrence of any biological phenomenon.

One possible objection is that while the truth (or falsity) of empirical adaptationism per se has no explanatory value, testing this general claim requires testing specific hypotheses about the causal role of natural selection in the evolution of particular traits. The results of such tests would contribute to explaining the form and distribution of those particular traits. This argument is problematic because it seems to assume that testing empirical adaptationism is a *necessary* condition for testing hypotheses about the evolution of particular traits when this is actually not the case. Since the truth (or falsity) of empirical adaptationism has no bearing on why a particular trait has evolved, biologists do not need to test empirical adaptationism in order to pursue and test hypotheses about the evolution of particular traits.

6.3 Epistemic value

Resnik (1997) argues that Sober and Orzack's long-run test of empirical adaptationism is valuable because it can "increase our knowledge about evolutionary trends" (Resnik, 1997, p. 46). If testing empirical adaptationism can increase our biological knowledge, then it seems to have epistemic value.

There are two issues with this proposal. First, it is not clear what exactly those "evolutionary trends" refer to. In my view, they refer to nothing but whatever is already described in various formulations of empirical adaptationism, such as the overall relative causal importance of natural selection in evolution. If this is the case, then it leads to the second issue, that is, it remains unexplained *why* it is scientifically valuable to have

knowledge about these trends. Failing to answer this question is tantamount to saying that it is scientifically valuable to test empirical adaptationism because it is scientifically valuable to know the result of such a test, which merely begs the question.

It may be argued that testing empirical adaptationism is valuable for those who want to conduct such a test because it satisfies their curiosity, and there is no need to ask further what the value of such curiosity is. Notice that this justification focuses only on the value of testing empirical adaptationism in terms of satisfying *individual curiosity*, but it says nothing about the value of such a test to science in general and biology in particular. An inquiry that arouses the curiosity of certain individuals may not be of scientific value. For example, an individual might want to know the center of gravity of all the humans on Earth, but knowledge of such a fact (if there is such a fact at all) does not seem to have any scientific value. By the same token, testing empirical adaptationism may be interesting to some researchers, but this does not automatically demonstrate why it is *scientifically valuable* to know the result of such a test. If we view scientific research as a social practice and scientific knowledge as social knowledge (Longino, 1990), then individual scientists need to provide further justification about why certain questions of interest to themselves are scientifically valuable and hence worth investigating and discussing within the scientific community.

6.4 Spin-off value

Not all scientific controversies can be resolved in the end. In many cases, participants in a scientific debate simply lose their interest and move to other topics (Kovaka, 2017). Nevertheless, these debates usually promote many meaningful discussions along the way,

hence creating great spin-off value. In the case of empirical adaptationism, one may concede that there is no conclusive answer with respect to its correctness, but still contend that the debates surrounding empirical adaptationism have inspired many in-depth discussions about a number of important topics in evolutionary biology. Given this, it seems reasonable to say that testing empirical adaptationism has some spin-off value.

Historically speaking, there is some element of truth in the above claims. For example, given Orzack and Sober's formulation of empirical adaptationism, evaluating the correctness of this thesis inevitably involves assessing the validity of the optimality approach in evolutionary research. This awareness has motivated them to publish a series of papers with the aim of clarifying how to properly construct and test an optimality model (Orzack & Sober, 1994b, 1994a, 1996), which are in no doubt scientifically valuable for evolutionary research. But facts like these do not justify the necessity of *continuing* the debates over empirical adaptationism or trying to test its correctness. Potochnik (2009) has convincingly shown that the fate of optimality modeling is not necessarily linked to that of empirical adaptationism. No matter whether empirical adaptationism is testable or not, and if it is testable, no matter whether it is true, the centrality of various uses of optimality models ensures a continuing role for the optimality approach in evolutionary research. Hence, stopping the debate about the truth of empirical adaptationism will not hinder the study of optimality modeling. In fact, much confusion can be avoided if studies like this can be detached from the debates over empirical adaptationism.

7. Rethinking the value of scientific debates involving overall relative causal importance

As mentioned before, a major theme of empirical adaptationism involves comparing the overall relative causal importance of natural selection and other evolutionary factors. The notion of overall relative causal importance is actually the combination of the notions of *relative causal importance* and *relative frequency*. The notion of relative causal importance is involved in the case where the production of a phenomenon is influenced by more than one causal factor and different factors may make different amounts of causal contributions to the focal phenomenon. A typical example is the case where a particle is accelerated by two forces acting in the same direction. One of the two forces can be regarded as a more important cause if it makes more causal contributions to the acceleration of the particle. The notion of relative frequency is involved in the case where there exist multiple, alternative accounts of a domain of phenomena but each of them can only account for a proportion of the phenomena in that domain (Beatty, 1997; Kovaka, 2017). Proponents of different accounts may debate what proportion of cases each account correctly describes, or which account covers a larger proportion of cases in a domain. For example, speciation can occur via different mechanisms, and evolutionary biologists and systematists have argued about the relative frequency of different modes of speciation. The notion of overall relative causal importance is a combination of the above two notions, because it concerns not only whether a factor plays a more important causal role in the production of particular instances of a type of phenomena, but also how often that is the case in the relevant domain.

Debates involving the notion of overall relative causal importance are actually quite common in scientific research. For example, in the nature-nurture debate, researchers argue about whether genes or environmental factors generally play a more important role in human development; in the niche-neutral debate, ecologists disagree about whether niche-based processes or neutral processes are generally more important in structuring ecological communities (Chase, 2014); in the field of cultural evolution, there is the debate about whether cultural transmission is generally more influenced by preservative processes or transformative processes (Acerbi and Mesoudi, 2015). All these debates concern the overall relative causal importance of different factors with respect to the totality of phenomena in a domain, and participants in these debates usually take the value and necessity of engaging in such debates for granted. However, my analysis of the case of empirical adaptationism has shown that this kind of "taking-for-granted" can be very problematic. On the one hand, in many cases it is just impossible to compare the relative causal importance of different factors in an intelligible way. On the other hand, even when this kind of comparison is possible, the sheer generality of debates involving the notion of overall relative causal importance may leave us unclear about the value of such debates, especially given the fact that the relative causal importance of different factors in a domain can be very context-dependent and may change from case to case. The applicability of these problems to debates involving the notion of overall relative causal importance should be assessed case by case. However, the general lesson is that scientists should change their *default* attitude towards such debates. Instead of assuming that debates involving the overall relative causal importance of different factors are self-evidently necessary and valuable, scientists should evaluate, case by case, the value and

necessity of engaging in such debates. When an alleged empirical debate involves claims that are confusingly vague, or when it is not clear what the scientific value of such a debate is, it is better to stop and think about whether it is worthwhile to step into this debate and whether there is a more productive way to structure the discussion.

8. Conclusion

As its name indicates, empirical adaptationism is typically described as an empirical claim about nature, a "genuine scientific hypothesis" that can be and should be tested in the long run. In this chapter, I have challenged both the testability of empirical adaptationism and the scientific value of testing such a general thesis. I have identified a series of conceptual and methodological difficulties that may well undermine the testability of empirical adaptationism. I have also shown that those who argue in favor of testing empirical adaptationism have yet to demonstrate the distinctive value as well as the necessity of conducing such a test.

The core of empirical adaptationism is to privilege the causal role of natural selection in evolution. Since the course of evolution is usually influenced by multiple evolutionary factors, it is not surprising that this privileging has led to great controversy. The fact that the debate about empirical adaptationism is notoriously difficult to resolve suggests that we may have asked the wrong question. Instead of asking "Which evolutionary factor is generally more important?", in future research it may be more productive to ask "How do different evolutionary factors interact with each other to influence the course of evolution?".

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